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The Natural History of Enewetak Atoll

Volume I The Ecosystem: Environments, Biotas, and Processes

United States
Department of Energy

Office of
Energy Research

Office of Health and
Environmental Research

Ecological Research
Division

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Volume I

The Ecosystem: Environments, Biotas, and Processes

Top: Aerial view of Enewetak Atoll from an altitude of 10,000 ft looking north. The wide south passage to the lagoon is at the bottom of the picture. The three islands to the right of the passage are Enewetak, Medren, and Japtan. The deep east pass is seen between Medren and Japtan. The five southwest islands are seen to the left of the wide south passage. Ikuren is the first one. North of these islands is the shallow southwest pass. The Atoll is elliptical in shape measuring about 41 km from north to south and 33 km from east to west. [Photography by P. L. Colin.]

Bottom: Aerial view of the northern end of Enewetak Island showing the cluster of buildings of the Mid-Pacific Research Laboratory. The quarry is visible on the reef flat. The small island immediately to the north is Bokandretak. [Photography by E. S. Reese.]

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The Natural History of Enewetak Atoll

Volume I The Ecosystem: Environments, Biotas, and Processes

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1930

[Photograph by Annabelle Lyman.]

Bok in, kōn menninmour ko im menin eddōk ko ion Enewetak, ej kein kememej im kautiej ri Enewetak.

This volume on the natural history of Enewetak Atoll is dedicated to the people of Enewetak.

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Foreword

As activity and funding at the Mid-Pacific Research Laboratory began to diminish in the early 1980s, it seemed fitting that a synthesis be prepared of the three decades of research that had been conducted at this Laboratory on Enewetak Atoll. For 30 years the Atoll served as a convenient, accessible location for studies of Mid-Pacific island ecosystems, and several hundred scientists utilized the facility. Primary funding was provided by the Office of Health and Environmental Research, Ecological Research Division, U. S. Department of Energy (formerly the Atomic Energy Commission and the Energy Research and Development Administration).

This is an attempt to synthesize in two volumes the results of the Mid-Pacific Research Laboratory studies that have been published in hundreds of widely dispersed publications. It is hoped that present and future scientists involved in studies of Mid-Pacific islands will find this synthesis a convenient resource for their research.

Considerable time and effort were expended by many contributors to make this synthesis possible. Thanks are extended to all these authors for their manuscripts. Special appreciation is expressed for Dr. Dennis Devaney's dedication in filling gaps in the taxonomic descriptions of several invertebrate groups. This publication would not have been possible, however, without the determination and persistence of Dr. Ernst Reese in organizing and collecting the material. Deepest gratitude is acknowledged for his conscientious efforts.

Helen M. McCammon, *Director*
Ecological Research Division
Office of Health and Environmental Research
United States Department of Energy

Acknowledgments

Many people have contributed in many ways to the production of these two volumes. Regardless of the nature of the contribution, everyone listed below has given thought and time, that most precious commodity of thinking individuals, to bring *The Natural History of Enewetak Atoll* into publication. Authors of the chapters are not listed separately, even though, in most cases, they critically read other chapters. No doubt we have overlooked many who have contributed in important ways, and for these oversights we apologize. To all of you we wish to extend our deepest thanks.

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Preface

The two volumes of *The Natural History of Enewetak Atoll* summarize research done at the Mid-Pacific Research Laboratory from 1954 to 1984 under the auspices of the Department of Energy. The history of the laboratory and the reasons for its support by the United States Department of Energy are described in Chapter 1 of Volume 1.

Over a thousand persons—established scientists, their assistants, and graduate students—conducted research at the laboratory during the 30-year period. Their efforts resulted in 223 publications. These have been collected in four volumes of reprints entitled *Mid-Pacific Marine Laboratory Contributions, 1955–1979*, U. S. Department of Energy, Publication NVO 628-1. The laboratory has continued operation on a limited scale to the present. A collection of papers recently appeared in the *Bulletin of Marine Science*, Volume 38, 1986.

Much of the research conducted at the laboratory was on the marine environment. The reason was that the majority of scientists applying to work at Enewetak were marine biologists. For many, this was the first opportunity to study the biota of a coral atoll. Fewer studies were conducted in the terrestrial environment and its biota. Nevertheless, as these volumes attest, the coverage is amazingly complete and thorough, and there are few, if any, studies of an equivalent ecosystem that equal the total research effort reported in these volumes.

Volume I provides a synthesis of the research carried out under the subject headings of the respective chapters. Certain of the chapters, e.g., those on geology, subtidal and intertidal environments and ecology, and those on reef processes and trophic relationships, summarize a great diversity of research carried out by many scientists for many years. In contrast, the chapters on meteorology and oceanography summarize research carried out under one integrated program involving fewer scientists working over a shorter period.

Volume II of *The Natural History of Enewetak Atoll* provides information on the taxonomy of animals and plants known to occur at Enewetak Atoll. This taxonomy represents a fulfillment of one of the first assignments to the laboratory—to determine the scientific names of the biota of the atoll. The collections on which the checklists in each chapter are based are housed at the Bernice P. Bishop Museum in Honolulu and the U. S. National Museum of Natural History, Smithsonian Institution, Washington, D. C.

In addition to the species checklists, each chapter in Volume II provides a succinct summary of the biota with respect to endemism, range extensions, and other features that set the Enewetak biota apart from those one might expect to find on equivalent Indo-Pacific islands. This compendium of taxonomic information for an atoll should prove of immense value to scientists interested in biogeography and evolutionary biology of island ecosystems for years to come.

One of the problems of editing these volumes has been the correct use of place names. In some cases authors used the military code names for islands while others used the native names. Even the native names have changed from early phonetic spellings to the spellings currently in use and preferred by the Enewetak people. For example, the name of the atoll has changed from Eniwetok to Enewetak, and, although the correct current spelling is used throughout, the old spelling occurs in older references and maps which appear in these volumes. Maps giving the military code names and the native names preferred by the Enewetak people are located in Chapter 1 of Volume I. Surprisingly, it is difficult to determine the exact number of islands. Due to the effects of storms, small islands are ephemeral, and two islands and part of a third were obliterated by nuclear explosions. Currently there are 39 recognizable islands, and these are shown on the map used throughout the book.

These volumes do not report on the extensive radiological surveys and studies which have been conducted by the Lawrence Livermore Laboratory, University of California, and the Radiation Laboratory, University of Washington, also under the auspices of the U. S. Department of Energy.

Dennis M. Devaney, senior editor of this volume, disappeared while collecting specimens off the Island of Hawaii on August 13, 1983. Dennis was doing what he loved best, collecting marine invertebrates, at the time of his death. He collected extensively at Enewetak, and he undertook the task of organizing the systematic chapters of Volume II. Beatrice L. Burch, Devaney's assistant at the

Bishop Museum, completed the task, and she has written the introduction to Volume II.

It is fitting that the two volumes of this book are dedicated to the people of Enewetak Atoll. They, like so many other human beings, were caught up by forces beyond their control and understanding in an immense cataclysm of human history. In a small way, this book stands as something good that has resulted from those years.

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Introduction

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The first volume of *The Natural History of Enewetak Atoll* provides a summary of the research carried out over the 30-year period from 1954 to 1984. The frontispiece illustrates the dramatic contrasts between the immensity of the lagoon and the seemingly fragile necklace of small islands which surrounds it, and also between the sea condition on the windward, seaward side of the reef and the relatively sheltered waters of the lagoon.

The first chapter discusses the history of research at Enewetak Atoll. The reasons behind the establishment of the Enewetak Marine Biological Laboratory are described. The authors, Philip Helfrich and Roger Ray, have been associated with activities at Enewetak from the very early days. They conferred with Robert W. Hiatt, the first director of the laboratory. In Chapter 2, Robert C. Kiste, a foremost authority on the people of Micronesia, provides a history of the Enewetak people to whom these volumes are dedicated.

The next four chapters deal with the physical environments of Enewetak Atoll. In Chapter 3, Patrick L. Colin describes the physiography of Enewetak. Colin served as resident scientist in charge of the laboratory from 1979 to the end of 1983 when all resident scientific staff left the atoll. Following the description of the atoll, Byron L. Ristvet, a frequent scientific visitor to Enewetak, provides a summary of the geology and geohydrology in Chapter 4. Next, in Chapter 5, Marlin J. Atkinson describes the oceanography. Under the direction of Stephen V. Smith, Atkinson participated in an important study of the lagoon circulation. Chapter 6 on the meteorology and atmospheric chemistry is the final chapter in the group of chapters dealing with the physical environment of Enewetak Atoll. Written by John T. Merrill and Robert A. Duce, the chapter is based on the results of the SEAREX Project. Duce served as the director and principal investigator of the project.

The next four chapters are devoted to the marine ecosystem and its biota. They summarize the large amount of research carried out at the Mid-Pacific Research Laboratory in the marine environment. All of the authors were frequent visitors to the laboratory, and they have done a splendid job of reviewing the research carried out in their area of interest. In Chapter 7, Patrick L. Colin describes the subtidal environments of Enewetak and reports on the research done on the subtidal biota. This is followed in Chapter 8 by Alan J. Kohn's masterful summary of research in the intertidal environment. Kohn has been a student of tropical intertidal ecology for 30 years. He tackled a particularly difficult task because of the extensive study of the intertidal environment and its biota by many scientists over the years.

Chapters 9 and 10 deal with processes and relationships in the marine environment. In Chapter 9, James A. Marsh, another frequent visitor to the laboratory and a recognized authority on coral reef processes, reviews the extensive work which was carried out at Enewetak on the community metabolism of coral reefs and related topics such as calcification processes, nitrogen and phosphorus cycles, and the role of detritus in the ecosystem. Nelson Marshall and Ray P. Gerber extend the ecosystem approach in Chapter 10 to include the entire atoll. They discuss the trophic relationship between the shallow reefs and the lagoon. Both Gerber and Marshall conducted research at Enewetak.

The final three chapters are devoted to the terrestrial environment. Because fewer scientists applied to conduct research in the terrestrial environment, less work was accomplished, and an integrated overview is not possible. In Chapter 11, I report on the life history, behavior, and ecology of land crabs, review what is known about atoll soils, and conjecture on the carrying capacity of an atoll such as Enewetak. For a description of the vegetation, the reader is referred to Chapter 3 in Volume II by Janet O. Lamberson. William B. Jackson, a frequent visitor to Enewetak over the years, and his co-workers Stephen H. Vessey and Robert K. Bastian report on their long-term study of the rodents in Chapter 12, and Andrew J. Berger summarizes our knowledge of the bird life of the atoll in Chapter 13. Berger, a noted ornithologist and the foremost authority on Hawaiian birds, made a number of trips to Enewetak.

I suspect that few readers will read this volume from cover to cover, but those who do will gain an appreciation for the complexity of the atoll ecosystem and a better

understanding of the intimate relationships between the seemingly fragile components of the ecosystem: the lagoon, the reefs, the islands and their biotas, all perched on a volcanic and coral pinnacle in the vastness of the Pacific Ocean. In the final analysis, however, the book will serve its purpose best if the reader comes away with more questions than answers and a desire to find the answers to these questions in future research on the natural history of coral reefs and islands.

Chapter 1

Research at Enewetak Atoll: A Historical Perspective

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INTRODUCTION

The Pacific theater of operations in World War II brought millions of military personnel to the tropical Pacific, and their activities on the Pacific Islands afforded close contact and awareness of the physiography and natural history of these small dots of land scattered in the vast expanse of ocean. This enhanced awareness, coupled with a recognized need by the military establishment for increased knowledge of Pacific Island areas, led to government-sponsored investigations, complemented by efforts of many individual scientists whose interest had been stimulated by wartime visits to these islands. In the postwar period, two activities of the U. S. government focused further interest on the coral atoll of the tropical Pacific and influenced the future of research at Enewetak Atoll (Figs. 1 and 2). The origin of the spelling "Eniwetok" is lost but would appear to be a phonetic rendering of what the people called their atoll. In 1973 it gave way to the current spelling, consistent with written Marshallese, and meaning "island which points to the east."

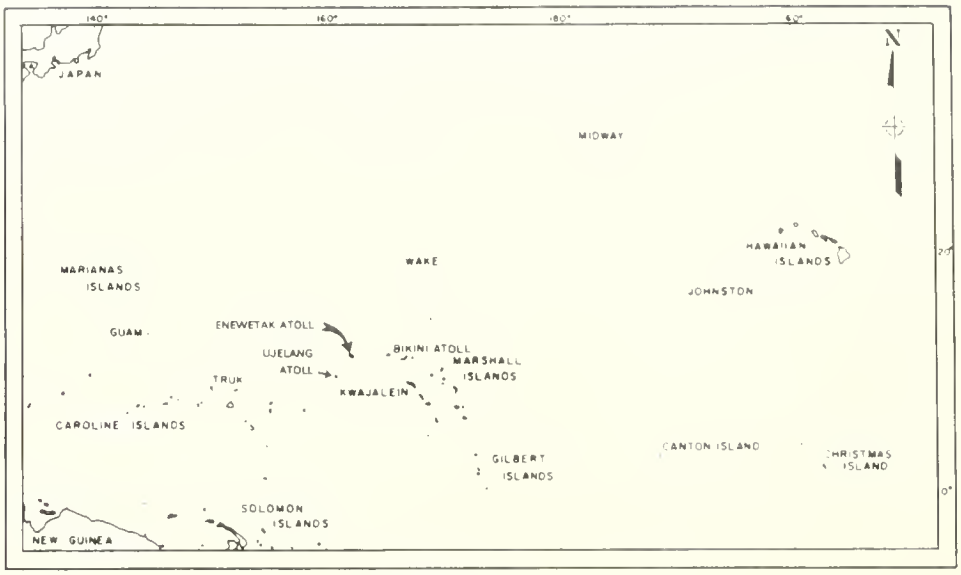
World War II demonstrated the importance of these small, scattered land masses to any military confrontation in the Pacific basin. After the war, the U. S. Navy moved to develop a series of permanent bases from among the many temporary wartime bases and outposts which had been established across the Pacific. With the prominent role of the Navy in developing and maintaining these bases, it is not surprising that the Navy's research arm, the Office of Naval Research (ONR), inaugurated a scientific program in the late 1940s aimed at a better understanding of atoll morphology and of all aspects of island life from microorganisms to human inhabitants. The ONR funded a series of expeditions in conjunction with the Pacific Science Association, many of which were to atolls in the central and western tropical Pacific. Arno Atoll in the southern Marshall Islands and Onotoa Atoll in the Gilbert Islands (now Kiribati) were subjects of intensive investigation in 1950 and 1953, respectively. Scientists involved in these atoll studies contributed to the establishment of the Eniwetok Marine Biological Laboratory (EMBL) on Medren Island, Enewetak Atoll, in 1954.

The second postwar activity which served to focus attention on the mid-Pacific area was the atomic weapons testing program in the northern Marshall Islands. Two atomic weapons had inflicted mortal damage upon Japan and had brought a precipitous end to the war in the Pacific. Military planners and strategists knew very little about this new and awesome strategic resource. Thus, an area was sought which might accommodate full-scale testing of atomic weapons. Neil Hines (1962) in his book *Proving Ground* describes the process of choosing the northern Marshall Islands as the testing site. First Bikini Atoll and then Enewetak Atoll became test sites, to be known together as the Pacific Proving Ground. National security considerations soon led to research and development testing and, with the impetus of the cold war, to the testing of thermonuclear weapons in these islands. In all, between 1946 and 1958, 43 nuclear devices were tested at Enewetak and 23 on Bikini—events which were to have profound and lasting environmental, social, and cultural effects upon these two atolls as well as others nearby. The nuclear testing program provided a setting, a focus of interest, and an opportunity for research in the northern Marshall Islands which eventually led to the establishment of the EMBL.

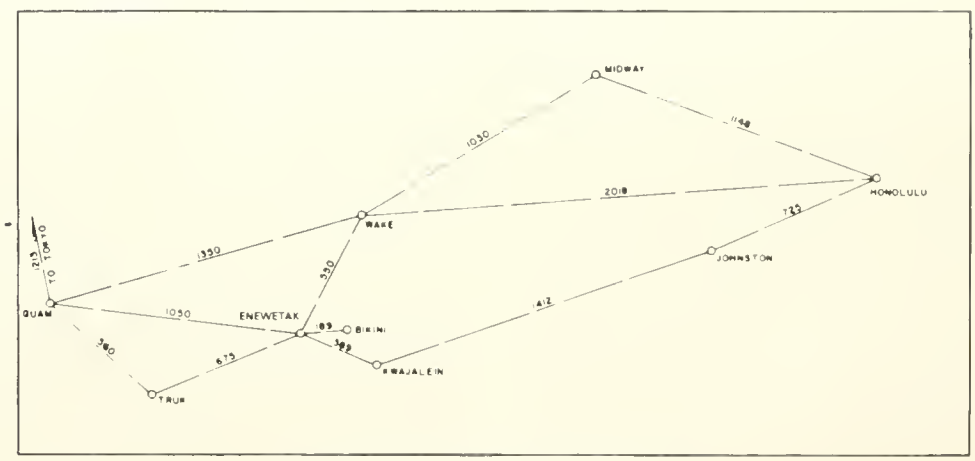
THE WEAPONS TESTING PROGRAM

Soon after the 1946 tests at Bikini (Operation Crossroads), which had been designed to assess the military significance of atomic weapons, the United States Congress created the Atomic Energy Commission (AEC), a civilian agency charged with responsibility for the research, development, testing, and production of nuclear weapons. This new agency was to become host and manager of the Pacific Proving Ground and, later, sponsor of EMBL.

Operation Crossroads was largely a seaborne operation, with logistic support from the naval base at



REGIONAL MAP



AIRLINE DISTANCES MAP

NO SCALE

Fig. 1 Regional and airline distances maps of the Pacific and the Marshall Islands showing location of Enewetak Atoll.

Kwajalein. It consisted of two tests, one an airdrop and the other an underwater detonation. The radiation and other effects of both of these tests—code-named Able and Baker—were largely confined to Bikini Atoll, with such fallout as left the Bikini area being deposited in areas of open ocean. The same could be said of the early development tests, which began at Enewetak in 1947. The selection of these atolls had been strongly influenced by their remoteness and by the predictability of wind conditions.

The 1954 operation, code-named Castle, was planned contemplating use of both atolls. Detonation of Bravo, the first test of Castle, drastically altered that plan. The explosive power (yield) of Bravo was more than twice that which had been predicted, and local winds carried the debris, or local fallout, directly across Bikini Atoll, contaminating much of the land area and rendering the control area and many of the experimental sites unusable for the remainder of the Castle operation (Hines, 1962). Some testing continued at Bikini, but Enewetak, after Bravo, took on even greater importance in the atmospheric nuclear testing program. During the period which ended on October 31, 1958, Enewetak was the site of 43 nuclear

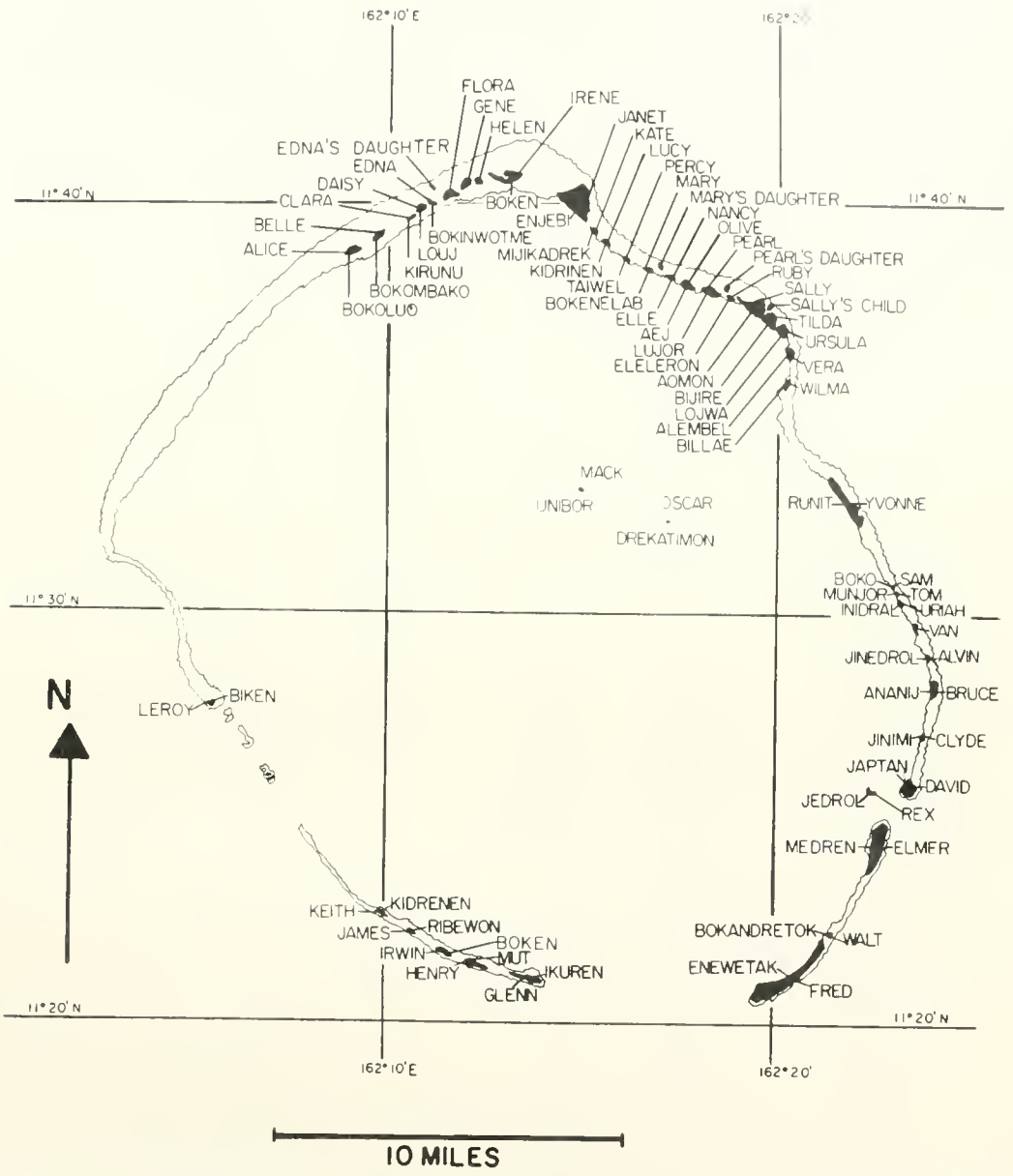


Fig. 2 Islands of Enewetak Atoll with Marshallese names shown on the lagoon side and English code names on the ocean side.

weapon tests. Enewetak, Medren, and Japtan Islands housed the command, administrative, logistic, and technical support facilities, and the islets in the northern and eastern portions of the atoll served as test areas. Table 1 lists the detonations at Enewetak, and Fig. 3 illustrates the test locations on the atoll.

The nuclear testing program required the mobilization of a vast assemblage of scientists, technicians, and support personnel and the establishment of laboratories, shops, and living quarters, in addition to port facilities and an air terminal to connect with a supply system extending through Hawaii to mainland bases as far as 8000 miles away. Test operations over more than a decade were conducted by a series of Joint Task Forces (JTFs), consisting of Army, Navy, Air Force, and AEC elements, in a coordinated operational command. The commander was a senior military officer of flag rank and had as his deputy a senior AEC scientist.

The test detonations were grouped in series which, typically, lasted several months. During the times between series—usually a year or more—the support apparatus continued to function. This availability of logistic and administrative support made it feasible to consider the establishment of a laboratory facility. The AEC interest in

TABLE 1

Nuclear Tests at Enewetak Atoll

Operation event name	Date	Type and height, ft	Yield	Location
Sandstone				
X-ray	4/14/48	Tower 200	37 KT	Janet, west tip
Yoke	4/30/48	Tower 200	49 KT	Sally
Zebra	5/14/48	Tower 200	18 KT	Yvonne, north end
Greenhouse				
Dog	4/7/51	Tower 300		Yvonne, north end
Easy	4/20/51	Tower 300	47 KT	Janet, west tip
George	5/8/51	Tower 200		Ruby
Item	5/24/51	Tower 200		Janet, north tip
Ivy				
Mike	10/31/52	Surface	10.4 MT	Flora
King	11/15/52	Airdrop 1500	500 KT	Yvonne, 2000′ N
Castle				
Nectar	5/13/54	Barge	1.69 MT	Mike Crater
Redwing				
Lacrosse	5/4/56	Surface	40 KT	Yvonne, north end
Yuma	5/27/56	Tower 200		Sally, west tip
Erie	5/30/56	Tower 300		Yvonne, by airstrip
Seminole	6/6/56	Surface	13.7 KT	Irene
Blackfoot	6/11/56	Tower 200		Yvonne, middle
Kickapoo	6/13/56	Tower 300		Sally, north tip
Osage	6/16/56	Airdrop 670		Yvonne, middle
Inca	6/21/56	Tower 200		Pearl
Mohawk	7/2/56	Tower 300		Ruby
Apache	7/8/56	Barge		Mike Crater
Huron	7/21/56	Barge		Mike Crater
Hardtack, Phase I				
Cactus	5/5/58	Surface	18 KT	Yvonne, north end
Butternut	5/11/58	Barge		Yvonne, 4000′ SW
Koa	5/12/58	Surface	1.37 MT	Gene
Wahoo	5/16/58	Underwater 500		James, 7400′ S
Holly	5/20/58	Barge		Yvonne, 2075′ SW
Yellowwood	5/26/58	Barge		Janet, 6000′ SW
Magnolia	5/26/58	Barge		Yvonne, 3000′ SW
Tobacco	5/30/58	Barge		Janet, 4000′ SW
Rose	6/2/58	Barge		Yvonne, 4000′ SW
Umbrella	6/8/58	Underwater 150		Glenn, 7400′ N
Walnut	6/14/58	Barge		Janet, 6000′ SW
Linden	6/18/58	Barge		Yvonne, 2000′ SW
Elder	6/27/58	Barge		Janet, 4000′ SW
Oak	6/28/58	Barge	8.9 MT	Alice reef, 3 mi SW
Sequoia	7/1/58	Barge		Yvonne, 2000′ SW
Dogwood	7/5/58	Barge		Janet, 4000′ SW
Scaevola	7/14/58	Barge		Yvonne, 561′ SW
Pisonia	7/17/58	Barge		Yvonne, 12000′ W
Olive	7/22/58	Barge		Janet, 4000′ SW
Pine	7/26/58	Barge		Janet, 8500′ SW
Quince	8/6/58	Surface		Yvonne, middle
Fig	8/18/58	Surface		Yvonne, middle

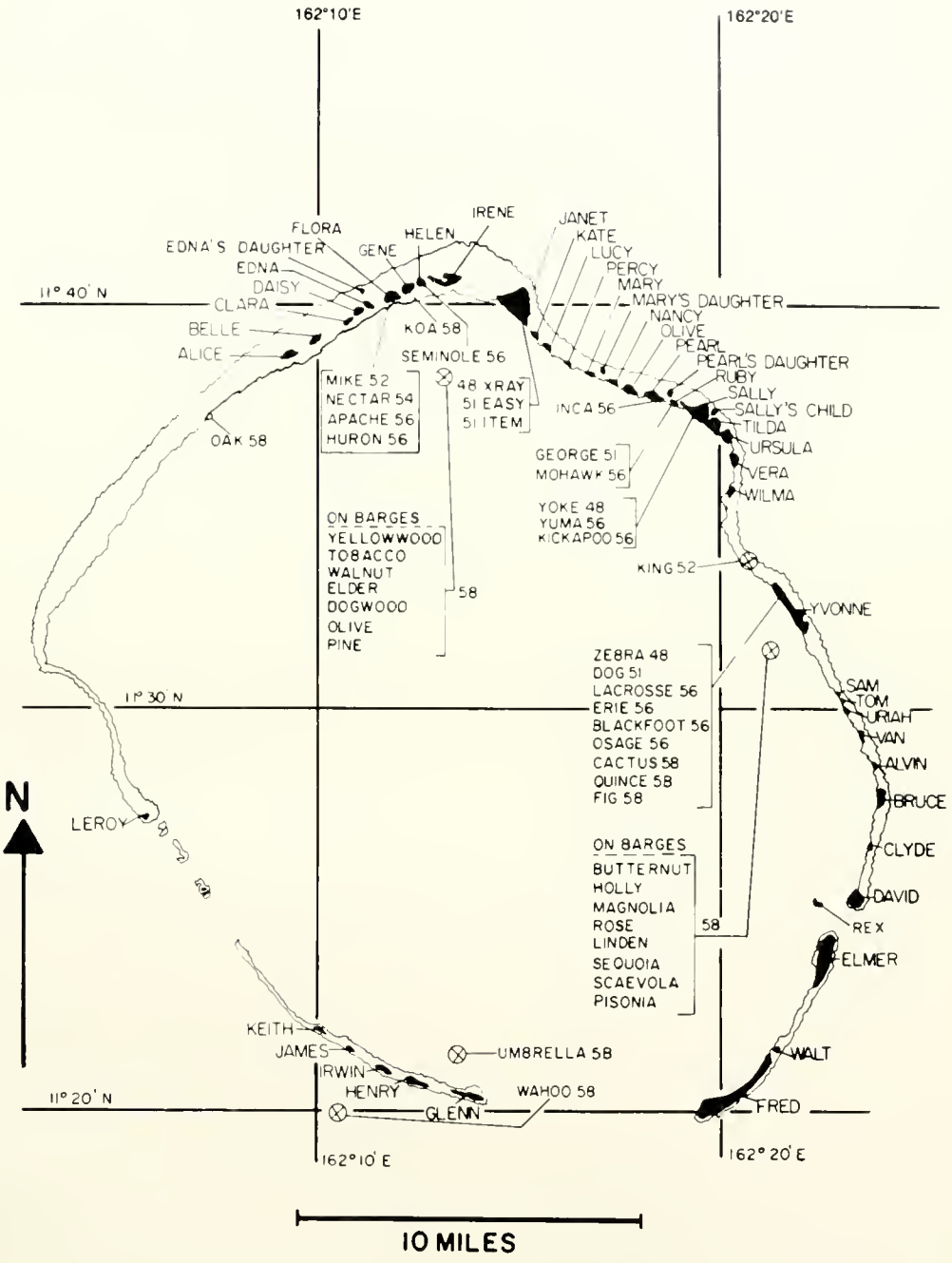


Fig. 3 Enewetak Atoll nuclear tests with name, year of detonation, and approximate locations.

expanding knowledge of the environmental setting in which the tests were being conducted provided the basis for discussions which led to the establishment of the EMBL.

ESTABLISHMENT OF EMBL

Of necessity, the nuclear testing program of the 1940s and 1950s was conducted in a climate of national urgency and classification security. Important scientific and strategic information had been lost to foreign powers in the immediate postwar period, and the pace of atomic weapons research and development had become a vital indicator of political power. In this environment, the establishment of a university-associated research laboratory, with its traditions of academic freedom and open publication of research results, was nothing less than remarkable. It reflected the enlightened scientific climate of the AEC and the AEC's concern regarding the long-term consequences of applica-

tions of nuclear technology. There was a need for more complete knowledge of the dynamic biogeochemical processes which might lead to the transport of radioactive contaminants in the atoll system to man. More fundamental was the acknowledged inadequacy of our understanding of the systematics and ecology of the highly diverse atoll biota. Early records of environmental monitoring during the test series included entries such as "red fish" and "green filamentous algae," reflecting the lack of any pertinent taxonomic descriptions of the local biota. The College of Fisheries of the University of Washington, under contract to the AEC, had conducted studies at Bikini and Enewetak of the interaction of environmental radioactivity with various species and had made substantial contributions to the literature regarding these nuclear-affected atolls (Hines, 1962). There remained, however, a need for a broader base of information about the systematics, ecology, and life history of the atoll flora and fauna.

Details of the discussions leading to the establishment of EMBL are unavailable. In the early 1950s, however, the eminent biologist, H. Burr Steinbach, then of the University of Chicago and later of Woods Hole Oceanographic Institution, was asked by Sidney Galler of the Office of Naval Research to travel to Enewetak Atoll to explore the feasibility of establishing a marine biological laboratory. Steinbach's trip and his subsequent report recommending the establishment of a laboratory on Enewetak Atoll were instrumental in AEC's action to contract with the University of Hawaii to establish and operate the EMBL.

The contract, signed on June 3, 1954, required the university to manage the laboratory and to direct and coordinate its scientific programs. Policy direction and sponsorship were provided by the Division of Biology and Medicine of the AEC Headquarters in Washington, D. C. Robert W. Hiatt, Director of the Hawaii Marine Laboratory, became the first director of EMBL. The first orders of business were to provide supplies, equipment, and work areas for visiting investigators and to establish a reference collection of animals and plants with an ecological index for their use.

To facilitate scientific investigations of terrestrial and intertidal biota, two islets on Enewetak Atoll—Ikuren and Mut—were set aside as reserves for the exclusive use of EMBL scientists. This was done to ensure that a continuously available source of typical fauna and flora would be protected, to the extent possible, from proving ground activities. During these early years, EMBL scientists were permitted to use the laboratory only in the intervals between test series. However, marine scientists from the University of Washington Applied Fisheries Laboratory, under separate contract to the AEC, were in residence during the actual test events. Their work at Enewetak and elsewhere in the Pacific is recounted by Hines (1962) and is reported in numerous published papers.

The laboratory was first quartered in a rectangular metal building, with an aquarium lanai, located on the southwest shore of Medren Island. The building was equipped with a simple seawater system, a single air-conditioned instrument room containing microscopes, a small library, and an assortment of nets, diving gear, and other field equipment. Being a sponsored tenant in the proving ground—which in peak periods accommodated hundreds of scientists, technicians, and support personnel—the laboratory enjoyed superb facilities for dining, housing, recreation, and medical care.

During the 1950s, 1960s, and early 1970s, the laboratory was operated on a part-time basis, with the active periods generally dictated by university class schedules. Thus, most investigators visited during the summer months and the periods of winter or spring academic holidays. Also during this period, visit authorizations were restricted to male U. S. citizens who had passed a security screening. Travel to Enewetak from Honolulu was by military or military charter aircraft. The flight time from Honolulu to Enewetak was about 10 hours, usually with stops at Johnston Island and at Kwajalein and/or Wake Island. It is noteworthy that, despite considerable resistance to the invasion by women of what had been traditionally an exclusively male territory, arrangements were made to accommodate the eminent zoologist E. Alison Kay at the Enewetak Laboratory in December 1970. Her arrival signaled a new era in which the merits of the scientific research proposed were the only criteria for acceptance of a researcher at EMBL.

Initially, the research emphasis at EMBL was toward the establishment of a reference collection of the local marine flora and fauna. This was accomplished by specialists, who made extensive collections of particular groups of animals and plants, identified the individual specimens (including those new to science), labeled, cataloged and preserved them, and placed them in the laboratory collection room. To complement the reference collection, a small library was established on site, providing convenient access not only to published references and texts but also to the works, both published and unpublished, of visiting investigators. Notices placed annually in the journal *Science* served to call this facility and its superb atoll environment to the attention of the community of marine scientists. This early research and subsequent publicity regarding the EMBL facility, combined with the availability of modest research grants, brought an enthusiastic response. From 1954 until this writing, 1028 scientists have worked at Enewetak, many returning for several periods of field collection and investigation. Notable was the response of temperate zone biologists who had not previously worked in the tropics. Entering the strikingly clear lagoon waters for the first time, with no more complex equipment than a face mask, was an exciting experience. Examination of a coral pinnacle, with its enormous diversity of organisms, brought a whole series of new dimensions to the work of these scientists. The limitations of the physical facilities and the remoteness of the EMBL field station were offset by an abundance of exciting research opportunities and virtual freedom from the pressures and distractions of campus life. These features resulted in a level of scientific productivity unequaled in the experience of most researchers.

The original EMBL building eventually proved inadequate to the needs of the scientists and in 1956 was expanded to include an extension for storage and a 4′ × 20′ concrete tank to hold experimental animals. Further expansion of the laboratory occurred in 1959 when Albert L. Tester of the University of Hawaii initiated a major program in shark physiology and behavior. For this program, two interconnected parallel tanks were constructed, which allowed sharks to swim in an oval pattern. This facility permitted Tester and his colleagues to hold and condition sharks, to test their reactions to various chemical stimulae, and to elucidate some of the anatomical and neurological bases for their aggressive behavior.

Nuclear testing activities at Enewetak ended in late 1958 with the declaration by President Eisenhower of a moratorium (accompanied by a similar Soviet moratorium) on all nuclear testing. The 1958 moratorium, originally a 1-year commitment, was actually continued until September 1961. At that time, the Soviets suddenly resumed testing at a high rate. Even then, however, the United States, in its response, did not return to testing in the Marshall Islands. Although the AEC continued to administer the Pacific Proving Ground until it was transferred to the Navy in 1960, AEC gradually withdrew activities and support on Medren until EMBL was the only active facility on that island. This made support such as power, water, housekeeping and messing, and logistics difficult. In 1961 EMBL moved from Medren to Enewetak Island where an active support infrastructure still existed. The laboratory's new home became a building on the lagoon side of Enewetak Island, previously used as a recreation center (Figs. 4 and 5). This building was modified to provide two small air-conditioned rooms for the protection of instruments and chemicals. A rectangular aquarium was constructed in the center of the large main room which was enclosed on three sides and open to the lagoon. A seawater system was installed, and living quarters were provided for EMBL personnel and visiting scientists in a building across the lagoon road from the laboratory complex. Although adequate, this facility had one important drawback. Boat operations required the use of the utility pier at the northeast end of the island, making loading and unloading difficult, and necessitating the carrying of equipment and specimens between the pier and the laboratory. By 1969, another move was in order.

In this same year, the directorship of EMBL passed first from Robert W. Hiatt to Vernon E. Brock, and then, a few months later, to Philip Helfrich. Helfrich continued as director until January 1, 1975.

In 1969, military activities at Enewetak dictated another move for EMBL, this time to the vicinity of a large, three-story dormitory building which had been constructed on the ocean side, toward the middle of Enewetak Island. The new location was a complex of aluminum buildings, previously used as library, recreation center, and darkroom. This location was more desirable because of its proximity to sleeping quarters, food service facilities, and the boat launching ramp. In addition, it included a large, covered lanai—which was supplied with running seawater for aquaria—and two portable swimming pools used as holding tanks. With about twice the space that had previously been allocated, the new facility included a large general laboratory, a shop, photo darkroom, library, equipment room, communications room, a dive locker, and a separate building for the storage of hazardous chemicals (Fig. 6). In the early 1970s, EMBL acquired its own communication system, providing a voice and teletype link to the University of Hawaii.

MOVES TOWARD RESETTLEMENT

The year 1972 brought significant political developments which were to have a lasting effect upon the future of the people of Enewetak and upon the fortunes of EMBL. Political status talks had been going on for several years between the government of the United States and representatives of the people of the Trust Territory of the Pacific Islands (TTPI). These talks were aimed at ultimate termination of the United Nations trusteeship over the Micronesian Islands (with the United States as trustee) and the establishment of one or more new and independent self-administering political entities. During the 1972 talks, responding to the pleas of the people of Enewetak for the return of their home islands, the United States took the first steps toward that return. In April, Ambassador Hayden Williams, the President's personal representative to the talks, was joined by High Commissioner Edward Johnston of the TTPI in a public statement of U. S. intentions. It provided that military use of Enewetak would shortly be completed, thus permitting the atoll to be returned to the administration of the Trust Territory, and that steps necessary to rehabilitate the islands for resettlement could then begin.

Later in 1972, the AEC's Nevada Operations Office, using the resources of its national laboratories and contractors, mounted a massive radiological survey of Enewetak Atoll as a preliminary step toward cleanup and rehabilitation. These activities are described in official reports (U. S. AEC, 1973; U. S. DOE, 1982; Holmes and Narver, 1973; and U. S. DNA, 1975). Although EMBL did not participate directly in either the 1972 survey or the cleanup, the director and other scientists consulted and assisted in many ways. While applied science and engineering were at work to restore the atoll, the basic studies of EMBL continued apace. Although this tiny, remote research station might have been overwhelmed by the enormity of the cleanup effort (thousands of men, over 3 years, at a cost of more than $100 million), those responsible in the AEC (now the U. S. Department of Energy) and the U. S. Defense Nuclear Agency (DNA), recognized the lasting worth of the science program and saw to it that the laboratory's interests were protected.

In 1978, the U. S. Coast Guard LORAN Station, which had occupied a complex of buildings at the eastern end of Enewetak Island, was closed. By agreement with DNA and with the people of Enewetak, DOE obtained the

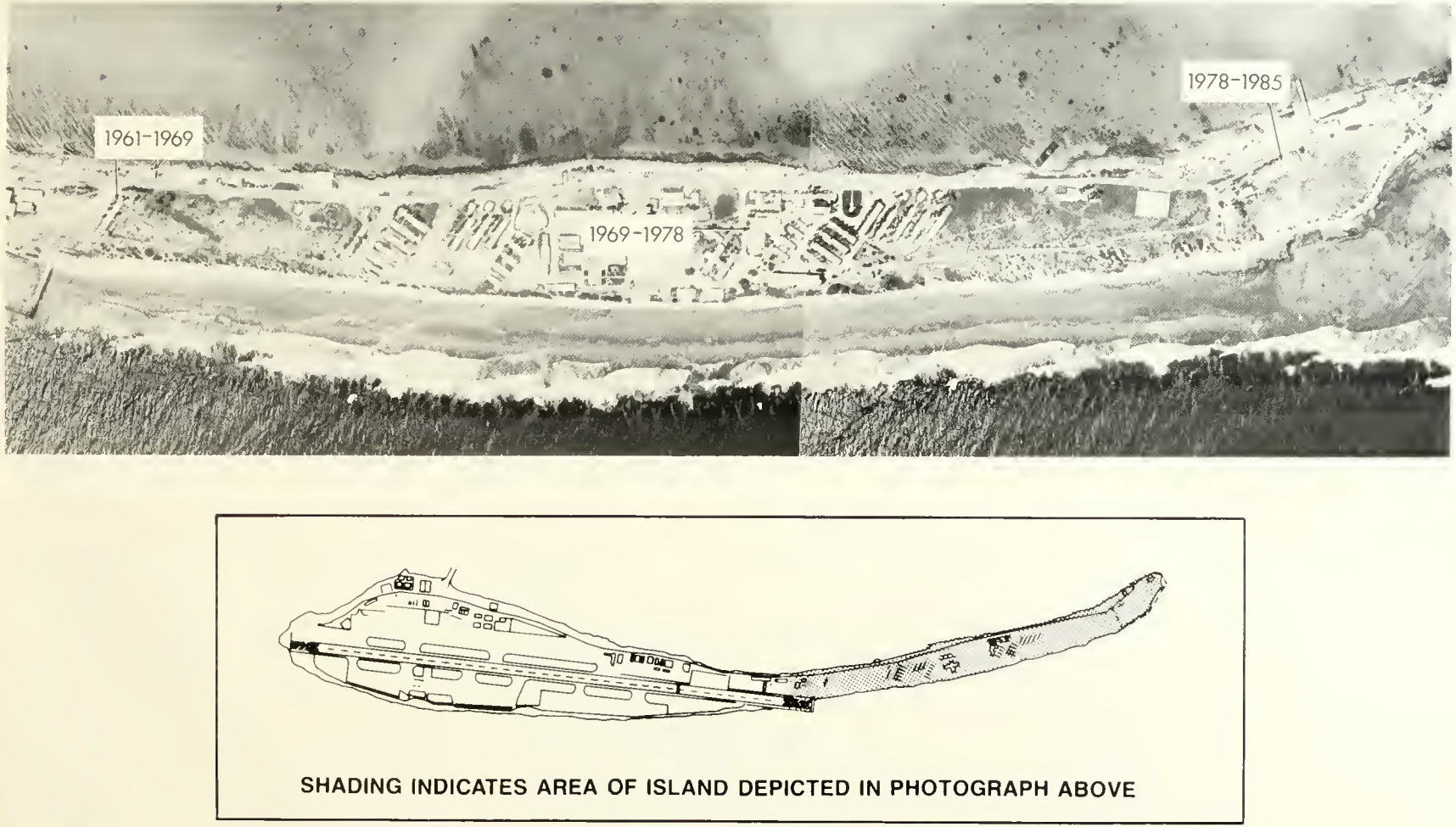


Fig. 4 Map and aerial photograph showing locations of laboratory sites on Enewetak Island.

Fig. 5 The second laboratory facility was located on Enewetak Island from 1961 to 1969. [Photo by E. S. Reese.]

long-term use of these facilities and allocated them to the laboratory (Fig. 7). Over the next 2 years, in anticipation of the demobilization of the cleanup force and the sharp reduction in available logistics and life support facilities, steps were taken to make the laboratory ready to "stand alone." The complex was augmented with several portable housing and laboratory units, and plans were made for local power, fresh and salt water systems, and other needed support. The new location was a considerable improvement, consolidating all operational and support activities in one location. The new facilities included a main air-conditioned laboratory building with work benches and equipment space, a library, communications room, dark room, reference collection room, and several storage rooms. Attached to the main building were a generator room and a storage shed. Four additional buildings provided sleeping quarters accommodating as many as 18 persons. Other buildings provided a kitchen, food storage, a chemistry laboratory, a scientific shop, a dive locker, a general maintenance shop, and a covered seawater lanai. A 50-foot tower on which two 600-gal tanks were located provided gravity feed for a seawater system. Good quality unfiltered seawater for this system was pumped from a former quarry in the reef.

Access to the lagoon for boats and personnel was provided by a conveniently located concrete ramp and a wooden pier. Laboratory boats were moored offshore or launched and retrieved from trailers at the ramp.

Fresh water was provided by catchment of rain from the roofs of several buildings and stored in four 10,000-gal cisterns. Diesel and gasoline fuels were stored in tanks on the lagoon side of the laboratory complex. These fuels, along with other supplies, were delivered to the laboratory approximately every 2 months by the DOE research vessel *Liktanur*, which was based at Kwajalein and supported DOE's environmental research, radiation protection, and medical programs in the northern Marshall Islands. Personnel, mail, and light cargo were usually transported via the Airline of the Marshall Islands (AMI) on approximately a biweekly schedule and occasionally on a chartered flight.

Fig. 6 The third laboratory facility was larger and in a more convenient location on Enewetak Island from 1969 to 1978. The name was changed to the Mid-Pacific Marine Laboratory (MPML) to emphasize the broader research purview of the laboratory. [Photos by E. S. Reese.]

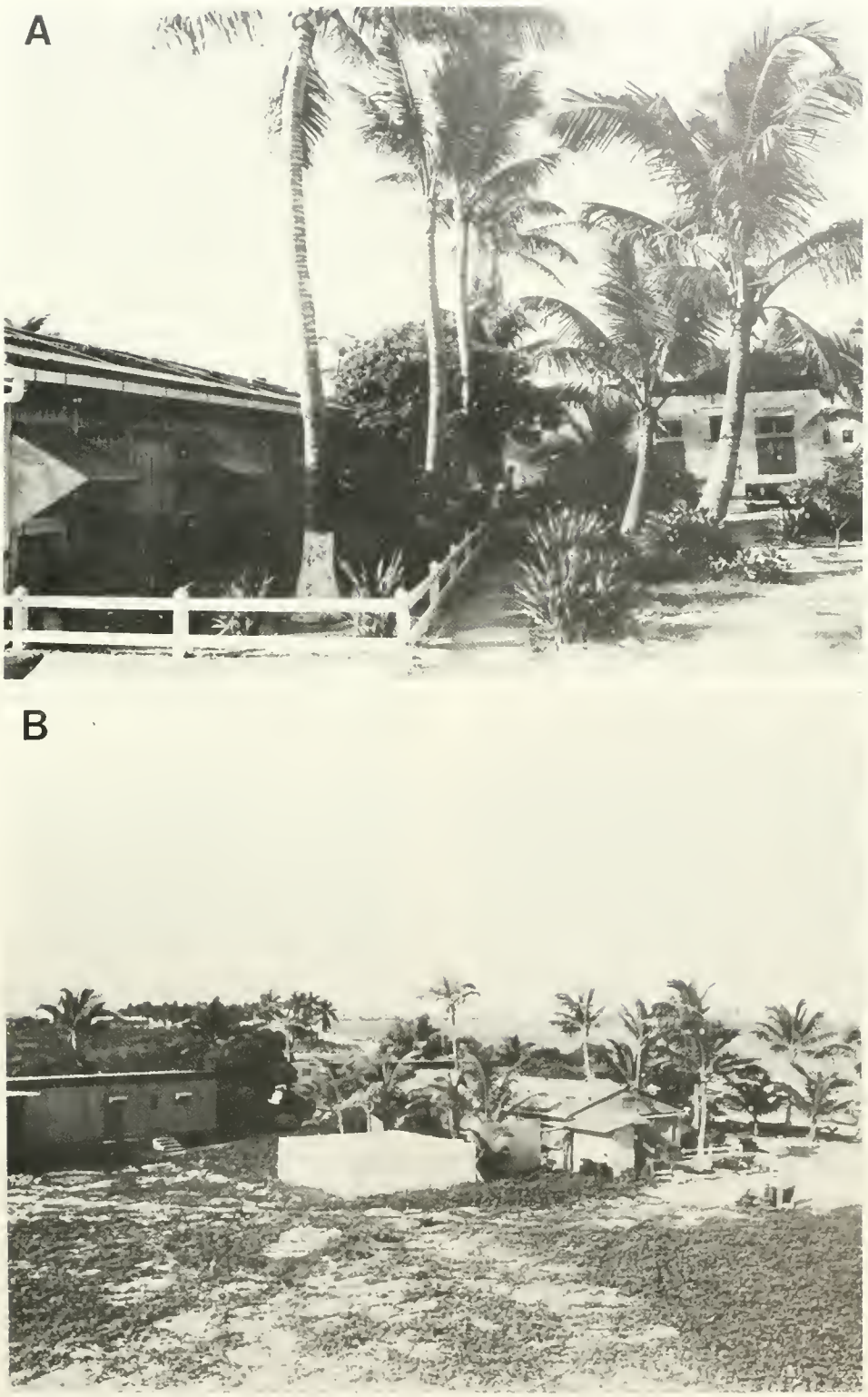


Fig. 7 The fourth and final location of the laboratory was in the former U. S. Coast Guard LORAN Station on Enewetak Island from 1978 to the present; a, The dormitory is to the left and the mess hall to the right; b, View of the laboratory complex from the 50-ft-high water tower with one of the cisterns in the foreground. The name was again changed to the Mid-Pacific Research Laboratory (MPRL) to note the inclusion of terrestrial as well as marine research. [Photos by P. Helfrich.]

RESEARCH EMPHASIS

There were two major periods of research at Enewetak conducted by the University of Hawaii under contract with DOE and its predecessors. During the first 20 years (1954 to 1974), the AEC supported independent research that was broadly aimed at increasing our knowledge of this rich and diverse coral atoll ecosystem. The rationale for supporting this broadly based research was that it was impossible to predict what aspects of the system might be most perturbed by the test activities or what the lasting effects of these perturbations might be. Thus, a broad spectrum of investigations was considered appropriate. In retrospect this was a wise choice because later events and decisions depended upon information resulting from this early research. Scientists from EMBL, with their acquired data base, were frequently called upon for advice and assistance, especially during the period of preparation of the atoll for the return of the Enewetak people. The modest cost of maintaining and operating the laboratory over these years provided the AEC with a bargain in science because the support systems were in place for AEC and defense department programs. The incremental cost of supporting the laboratory was, therefore, relatively small. The scientific research was accomplished at low cost because most of the participating scientists were salaried by their home institutions.

Much outstanding research was accomplished at EMBL (Fig. 8). The record of accomplishment is set forth in the volumes of collected reprints of scientific publications which were issued in 1976 and 1979 (U. S. ERDA, 1976; U. S. DOE, 1979). As knowledge of coral reef ecosystems advanced, it was deemed advisable to mount a major effort to understand the metabolism of an entire atoll (Fig. 8). Discussions and planning conferences culminated in the initiation of a major program in the summer of 1971 under the name SYMBIOS. This program lasted for 12 weeks and involved the research vessel *Alpha Helix*, 25 participating scientists, and numerous support personnel under the leadership of Robert Johannes. SYMBIOS was jointly sponsored by the National Science Foundation, the AEC, and the Janss Foundation. Its initial objective—to study the metabolism of an entire atoll—proved to be too ambitious, but a thorough study of the windward reef was accomplished and some major advancements were realized in our knowledge of reef metabolism. As with other research, this effort posed many new questions and challenges, and resulted in repeat visits to Enewetak by SYMBIOS scientists to further pursue work initiated in this landmark study. The results of SYMBIOS are summarized in Chapters 9 and 10 of this volume.

In 1972, the DNA began a series of studies to better understand cratering effects of nuclear explosions. Craters formed by the nuclear explosions of earlier years were analyzed by direct observation, seismic response measurements, and dynamic experiments utilizing chemical explosives. Scientists from EMBL were called upon to advise the defense department, especially upon the expected impact of their experiments on the marine environment. Later, following a strong protest and legal action by lawyers for the people of Enewetak, the dynamic experiments were canceled and only shallow coring of the atoll rim and seismic studies of the reef structure were pursued to complete this project.

The second period of research began with the reorganization of the laboratory in 1974. Following discussions with the Chairman of the Atomic Energy Commission, Dixie Lee Ray, a visit was made to the laboratory by an ad hoc advisory group, including officials and scientists from the University of Hawaii, the AEC, and several independent consultants. Chairman Ray had expressed an interest in reorganizing and upgrading the laboratory to a full-time operation, with research objectives more directly relevant to AEC interests. The advisory group met at Enewetak in February 1974 and later made brief visits to Bikini and to Majuro, the capital of the Marshall Islands. Participants were William O. Forster, Nathaniel Barr, and Charles Osterberg of AEC Headquarters; Roger Ray of the Nevada Operations Office of the AEC; Philip Helfrich of the University of Hawaii (Director of EMBL); William R. Coops of the Research Corporation of the University of Hawaii; Robert Hiatt of the University of Alaska (first Director of EMBL); and Glen Fredholm, an independent consultant. The advisory group: (1) articulated in some detail its recommended objectives for a laboratory agenda which would be responsive to AEC direction, (2) suggested that the field station at Enewetak be upgraded to full-time activity with a resident staff, and (3) recommended that the name of the laboratory be changed to the Mid-Pacific Marine Laboratory (MPML) to reflect its interest in a wider geographical area, including such areas as Bikini, where the AEC continued to have an active interest.

In March 1974, following the advisory group meetings, Roger Ray and Philip Helfrich returned to Majuro to meet with officials of the government of the Marshall Islands and with members of the Enewetak Municipal Council. The latter meetings were hosted by Micronesian Legal Services Corporation, counselors for the people of Enewetak. The Enewetak Council expressed its desire that the laboratory continue to function in the Enewetak community after the return and resettlement of the atoll residents. It approved the site of the Coast Guard LORAN Station as the ultimate home of MPML.

With the approval of reorganization and redirection of goals, the laboratory entered a new and productive phase. Support and encouragement of basic studies continued under AEC sponsorship, while mission-oriented research was being planned and implemented. The major AEC-oriented projects of the 1975 to 1980 period were (1) a study of the circulation of the Enewetak Lagoon, (2) research on the dynamics of groundwater resources of Enewetak Atoll, and (3) studies of ciguatera fish poisoning at Enewetak.

On Jan. 1, 1975, Philip Helfrich left the University of Hawaii and was replaced as director of MPML by Stephen V. Smith, who served in that capacity until 1977. During

Fig. 8 Research activities as MPRL; a, Researchers making observations with the aid of scuba equipment; b, Coral studies in the laboratory; c, Microscopic analysis of organisms collected from the reef; d, Researcher making observations on a shallow reef. [Photo credits unknown.]

Smith's tenure the three research projects mentioned above dominated the activities of the laboratory. A study of the oceanography of Enewetak Lagoon was prompted because—despite intensive studies of various facets of Enewetak's geology, physiography, biota, ecosystem dynamics, radiation contamination, etc.—only cursory information existed on the circulation patterns of the lagoon (Chapter 5 of this volume). This comprehensive study directed by Smith resulted in information on the physical and chemical dynamics of the entire lagoon. The topic of the second investigation was the dynamics of groundwater resources of Enewetak, a study that developed information vital to the returning Enewetak people who required uncontaminated water for drinking and agriculture. This investigation was directed by Robert W. Buddemeier (Chapter 4 of this volume). Ciguatera fish poisoning, the topic of the third study, had plagued the people of the Marshall Islands for many years, waxing and waning in an inexplicable manner. The return of the people and their dependency on fish for sustenance placed a special urgency on the results of this study that was directed by John E. Randall (Chapter 7 of this volume).

During 1975, the AEC was reorganized, and the functions pertinent to MPML were assigned to the newly formed Energy Research and Development Administration (ERDA). In turn, ERDA gave way to the U. S. DOE in 1977.

Resident managers were established at MPML on a year-round basis in 1975, and these individuals became integrated into the Enewetak community. This was an important aspect of MPML's operations because these scientists represented a benign, if not benevolent, element among the numerous government-sponsored activities related to the radiological survey, cleanup operations, and various medical and agricultural programs. The individuals who served as the resident laboratory managers were all exemplary in their dedication, and there were numerous examples of extraordinary service. From 1975 to 1977 the resident laboratory managers were Philip and Janet Lamberson.

In June 1977, Ernst S. Reese assumed directorship of MPML, replacing Smith. During Reese's tenure (1977 to 1979), the research on lagoon oceanography, groundwater dynamics, ciguatera, and other aspects of atoll research continued. Planning and implementation of the move to the former Coast Guard LORAN Station took place. In addition to continuing to fully support the research mission of MPML, the laboratory personnel cooperated in many ways with the DNA. A highlight of this cooperation was the production of an audio-slide presentation to acquaint the military personnel of the DNA with the natural history of a coral atoll and to describe the recreational opportunities offered by the atoll environment. There was also a cautionary note about the dangers of the atoll environment ranging from severe sunburn to the presence of sharks. The audio-slide presentation contained an important message about conservation of the atoll environment as well: observe and enjoy but do not destroy.

Following the cleanup, support services were withdrawn, and the laboratory was placed on a "stand alone" status, having to provide for all of its own life support and laboratory operations needs, with resupply from infrequent supply ships and light aircraft. During this challenging period, Reese was ably assisted by Victor R. Johnson and Maridell Foster and by several capable resident laboratory managers: Paul M. Allen, Michael V. DeGruy, and Gary Long (1977 to 1979). In 1979, Patrick L. Colin and John T. Harrison (1979 to 1983) took over the operation of the laboratory. Throughout this period the laboratory continued to accommodate a few visiting scientists as transportation and logistics could be arranged.

In 1979, with the cleanup of Enewetak nearing completion and the return of the atoll's residents imminent, a workshop was held at the Asilomar Conference Center, Monterey, Calif., to consider the future role of the laboratory and its relationship to the other DOE scientific programs in the Marshall Islands. The DOE headquarters sponsor at that time was the Division of Biomedical and Environmental Research under the direction of Helen M. McCammon. The DOE policy enunciated at this time signaled the ultimate phase down of the laboratory over the following 2 to 3 years and the determination that significant effort should be devoted to synthesizing the research product of the laboratory's entire history into a publishable work. The present volumes are the result. It was decided also that, to the extent that the laboratory continued active research programs during the phase down years, these should not be confined to the marine environment. This latter decision was reflected in yet another name change: MPML became MPRL, the Mid-Pacific Research Laboratory. In 1980, soon after the Asilomar meeting, Helfrich again assumed the directorship of MPRL.

For most of the time between 1977 and 1980, a large, joint military force was at Enewetak—with a peak population of about 1000 drawn from the Army, the Navy, the Air Force, civilian government agencies, predominately DOE and civilian contractors. Research at MPRL continued through this period and in some ways the laboratory thrived upon the ready availability of logistic support, especially frequent and dependable airlifts, and a generally harmonious relationship with the joint cleanup command. In fact, through the cleanup years, the resident manager of the MPRL facility met daily with the Joint Task Group Commander and his staff to discuss mutual interferences and mutual support. Many interesting aspects of the cleanup effort required an intimate knowledge of the atoll system, and the laboratory was often called upon for consultation and advice. Selection of a suitable site for lagoon disposal of debris, protection and exploitation of food resources, and the preservation of scientifically valuable artifacts were but a few examples. On one occasion a major earth-moving effort was planned for an island which had unexpectedly become a nesting ground for a very large flock of migratory birds. The laboratory's data base facilitated an immediate assessment of the length of time these birds would require protection, and it was possible to

reschedule the cleanup activities so as to have only a minimal effect upon them.

The atoll rehabilitation program consisted of the removal and disposal or isolation of debris and contaminated materials, the construction of homes and community buildings and facilities, and the planting of more than 30,000 coconut, pandanus, and breadfruit trees. The cost was over $100 million. In April 1980, a ceremony was held at Enewetak, commemorating completion of the cleanup and the return of 543 Enewetak people to their ancestral home. A short time later, the last elements of the Joint Task Group departed Enewetak, leaving the laboratory as the only American presence in the community.

Over the next 3 years, major emphasis was placed upon studies of a portion of the atoll ecosystem which had until then been largely unexplored—the soft lagoon substratum. This research was directed by Patrick L. Colin. Much of the fallout material which remained from the nuclear tests had settled in the lagoon floor, and the dynamics of this biotope were little understood. As a result of this research, a fresh perspective was acquired. What had formerly been considered to be a largely passive system into which materials were sedimented from the water column was revealed to be an area in which burrowing organisms were continually reintroducing material into the water column—a process which led to some revision of the understanding of important biogeochemical processes. Interest in these processes helped to stimulate interest, in 1981, in one more interdisciplinary initiative at Enewetak.

A significant improvement in understanding of the deeper sediments of the lagoon required direct observation and sampling, and these techniques required the use of a research submersible. With the cooperation of the Hawaii Undersea Research Laboratory, the research submersible *Makali'i* was made available for a period in the summer of 1981 (Fig. 9). Other sponsors of the expedition were the National Oceanographic and Atmospheric Agency (NOAA) and the DOE. The DOE support included use of the research vessel *Liktanur*. Fifteen scientists and seven support personnel participated in a program which included

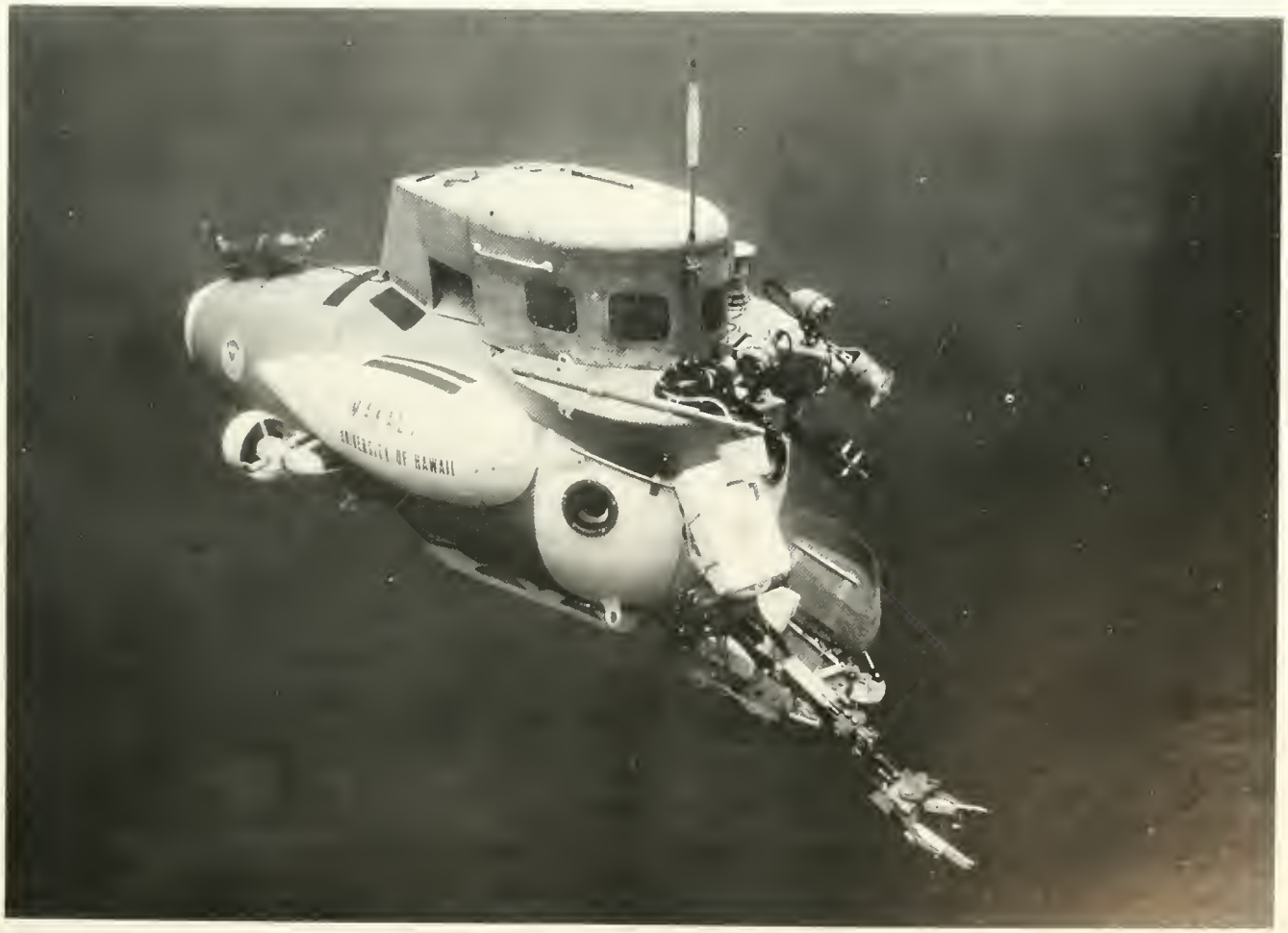


Fig. 9 The research submersible *Makali'i* operated by the University of Hawaii shown on one of its 53 research dives in the Enewetak Lagoon in the summer of 1981. [Photo courtesy of HURL Program, University of Hawaii.]

52 successful research dives between July 7 and Sept. 29, 1981. The results were presented in a special symposium of the Western Society of Naturalists in Los Angeles in December 1982 and were published in *Bulletin of Marine Science* (Harrison, 1985).

AN ERA ENDS

Although the plans for an autonomous laboratory after the 1980 departure of the cleanup forces were thoughtfully and thoroughly prepared and enthusiastically carried out, and despite the welcome that MPRL had received from the returning Enewetak community, its anticipated position as a permanent fixture in that community was not to be. At a time of constrained research dollars in the DOE, and with support grants from all sources limited, the cost of maintaining a resident staff and operating the MPRL facility as a self-sustaining field station became prohibitive. Support from the Division of Biomedical and Environmental Research was terminated in 1982, whereupon DOE's Nevada Operations Office sought and obtained funding for one more year through the DOE Office of Defense Programs. This additional year of funding permitted an orderly phase down of the laboratory activities and the preservation of some of MPRL's unique assets.

The reference collection which had been started during Hiatt's early tenure had grown and had been well preserved and cataloged. For several years this was accomplished through a contract with the Bernice P. Bishop Museum, under the able supervision of the late Dennis M. Devaney. The collections were carefully packaged and shipped to Hawaii to be placed in the temporary custody of the Bishop Museum. Early in 1985, negotiations were completed by the DOE with the Smithsonian's National Museum of Natural History and with the Bishop Museum for the permanent transfer of the reference collection to the latter institution. The MPRL's library and much of the laboratory equipment were transferred to Hawaii Institute of Marine Biology.

The remaining U. S. government activity at Enewetak is now conducted on a campaign basis, usually supported by the research vessel *Liktanur*. At this writing, however, two DOE contractor employees remain at the atoll, and the field station remains intact and capable of limited support. Philip Helfrich retains the title of Director of MPRL and, with modest funding from DOE, entertains inquiries from scientists who desire to explore the feasibility of continuing studies at the atoll. There is every indication that the people of Enewetak would welcome such visits.

ACKNOWLEDGMENTS

The wisdom and foresight of H. Burr Steinbach and Robert W. Hiatt and of those in the Office of Naval Research and the AEC who spawned and nurtured the idea of a research facility at Enewetak deserve special note. Time has proven that the decisions to establish, maintain, and support EMBL and its successors were wise and fruitful commitments which resulted in important contributions to our knowledge of atoll ecosystems and more broadly to marine science. Assuredly, there are still many unanswered questions, but just as surely new knowledge will continue to be built upon the foundation of about 250 published scientific papers which have resulted from research conducted at Enewetak Atoll over the past 30 years. The writers of this chapter, who have been partners in the administration and support of the laboratory for almost half of that period, record their hope that new ways will be found by interested scientists and their sponsors to continue, even on a limited scale, the exciting and rewarding experience of research at this remote and isolated atoll.

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Chapter 2

History of the People of Enewetak Atoll

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INTRODUCTION

The names of Enewetak and Bikini Atolls are linked in history, and they are well-known around the world because of their use as nuclear test sites by the United States. Indeed, once the atolls became available as research sites, a vast amount of research resulted; this volume is just one of the results. Most of the research has been in the biological and physical sciences, and the sheer volume of it has tended to obscure a very important fact—Enewetak and Bikini could be used for nuclear and other research purposes only after their indigenous human populations had been moved elsewhere. Much less is known about the people than about the flora, fauna, and physical properties of their atoll homelands. This chapter focuses upon the people of Enewetak. It examines their history, the structure of their culture and society, the ways they have coped with the colonial powers that governed the islands, and their response to their resettlement on Ujilang Atoll. Some mention is necessarily made of the Bikini community because the histories of the two peoples are intertwined.

Data about the Enewetakese are mainly derived from the research of four anthropologists, all of whom worked with the people after their relocation. Jack A. Tobin was the first. He served as Marshall Islands District Anthropologist between 1950 and 1957. He resided with the Enewetakese on several occasions, and portions of this work resulted in his doctoral dissertation (Tobin, 1968). In 1964, Leonard Mason and I spent several months on Ujilang, and during the academic year 1972–73, I was involved in a legal suit (to be discussed later) which involved the Enewetakese and the U. S. Department of Defense (Kiste, 1976). More recently, a younger anthropologist, Laurence Carucci, spent 1977 and 1978 with the Enewetakese, and he too produced a doctoral dissertation (Carucci, 1980).

THE ANCIENT PAST

The research findings of prehistorians and linguists indicate that the Marshalls and other islands of Micronesia were settled by peoples who migrated from the general area of island southeast Asia into the insular Pacific many centuries ago (Bellwood, 1979). Indeed this particular migration probably began about 5000 years ago. Reflecting the ancient migration patterns out of island southeast Asia, the Marshallese language belongs to the large Austronesian (also known as the Malayo–Polynesian) language family which is spread from Madagascar, through southeast Asia and across Micronesia, Polynesia, and many regions of Melanesia. Exactly when the early migrants arrived in the Marshalls is not known. The earliest archaeological date currently available for the Marshalls is from a site at Majuro Atoll which was occupied at the time of Christ. In all probability, future archaeological research will push the date for the settlement of the Marshalls further back in time.

No archaeological research has ever been conducted at Enewetak Atoll, however, and it seems safe to assume that remains of the past once deposited in its soil were obliterated with the preparations for and by the nuclear test program. The Enewetakese, however, have their own version of the distant past. According to their oral literature, they had always lived on Enewetak. In their own words: "We were there from the beginning." At the same time, their legends also recount how at least some of their ancestors purportedly came from Bikini, Ujae, Wotto, and other atolls also located in the northern Marshalls (Tobin, 1968).

Regardless of the time of the settlement of Enewetak, two things are certain. Enewetak Atoll is isolated, and once the ancestors of the current population were in place, they had relatively little contact with other communities. As a consequence, the language and culture of the Enewetak people became differentiated from those of other Marshallese, and the people did not identify themselves with the others. Indeed, they thought of themselves as a people who were separate and unique, "the people of Enewetak Atoll" as opposed to the islanders in the rest of the Marshallese archipelago.

The contact that the Enewetakese had with others, little as it was, was not limited to the Marshalls. The oral accounts associated with genealogies relate that some Enewetak people, mainly males, occasionally sailed to the south and west, contacting the ancient population of Ujilang (included in the Marshalls) and on to the high volcanic and culturally and linguistically different island of Ponape. Contact with Ponape was to continue well into historic times and up until World War II.

Long before the advent of Europeans, the people of Enewetak had developed a culture which represented a good adaptation to the limited atoll environment which is quite restrictive when compared to the high volcanic islands of the Pacific. The people were skilled navigators (an art which has been lost with the availability of travel on the vessels of foreigners), and they were expert builders of outrigger sailing canoes which were among the largest in the entire Marshalls. (Well into the 1960s, the Enewetak people were still constructing canoes that measured over 55 feet in length with masts that soared 30 feet above the vessels' decks.)

In the relatively dry northern Marshalls and with the poor soil of the northern atolls, terrestrial resources were quite limited. Subsistence resources from the land were limited to coconuts, pandanus, papaya, bananas, and arrowroot. One or two breadfruit trees produced poorly. None of these crops required much care, and the people were very casual in their attitude about their maintenance. A similar attitude was evidenced regarding domestic animals. A few pigs and chickens were allowed to more or less fend for themselves, and their flesh was mainly reserved for holiday occasions.

Thus, in part, ecological necessity had caused the Enewetak people to develop an economy which was heavily reliant upon marine resources. They knew the behavior and the monthly and annual movements of the large inventory of marine fauna. The fish of the lagoon and sea were caught, and expeditions were organized to collect shellfish, capture lobsters and turtles, and gather turtle eggs. In addition, several species of birds were also captured as food resources.

Shortly after the beginning of the German colonial era, old patterns were altered and the people became involved in the copra trade. Coconuts were converted to copra for cash and/or trade goods. Rice, flour, sugar, coffee, tea, canned meats and fish were eventually added to the diet.

Several other features of the people's lifestyle deserve mention. Like most atoll dwellers, the people located their residences on the largest islands of their atoll. In the case of Enewetak Atoll, only the two largest islands were inhabited: Enewetak Island in the southeastern quadrant of the atoll and Enjebi Island on the atoll's northern rim.

Although permanent residences were located on Enewetak and Enjebi Islands, the people were quite mobile within the atoll. Fishing and collecting activities penetrated every niche of the environment. Regular expeditions were made to all islands in the atoll to make copra and to collect food resources. Clearing brush and planting were done during these visits. Except for holiday seasons, it was not unusual for half of the population to be away from the two main islands as the people dispersed in pursuit of a livelihood and for pleasure. Such expeditions broke the monotony of life on a small island and provided relief from one's fellows.

SOCIAL ORGANIZATION

Although the people had a collective identity as Enewetakese when juxtaposed to other Marshallese, they were divided internally into two separate communities that resided on Enewetak and Enjebi Islands. Community is defined as "the maximum group of persons who normally reside together in face-to-face association" (Murdock, 1949). Members of the two communities intermarried and cooperated in a variety of activities. Each functioned, however, as a separate social and political unit, and its members had separate identities. The people of the Enewetak community called and thought of themselves as *riEnewetak* (the people of Enewetak Island) and those of the Enjebi community were *riEnjebi*, (the people of Enjebi Island).

The traditional settlement pattern of both communities was dispersed. Residences were located on separate land parcels known as *wato* and were scattered along both sides of a sand and coral roadway which ran parallel to the length of the lagoon beach. In most cases, a *wato* was a strip of land which cut across the width of an island from lagoon beach to oceanside reef. They varied in size from about 1 to 5 acres. Each *wato* had a name, and the people who lived on Kabnene *wato* on Enewetak Island were sometimes referred to as *riKabnene*.

The two communities had the same political structure. Each was headed by a hereditary chief known as *iroij* (Fig. 1). The chiefs directed the affairs of their respective communities, arbitrated disputes, and consulted one another with regard to concerns of the entire atoll and the total population's relations with outsiders (Fig. 2). In contrast to other Marshallese communities, which are organized around matrilineal principles, succession to the chieftainship was patrilineal, i.e., a man was succeeded by his eldest son; the eldest son was succeeded by his younger brothers in the order of their birth; and when the last of them died, the eldest son of the eldest son succeeded.

Like other Marshallese, the people of Enewetak Atoll were divided among several matriclans. The clans were named, and every individual automatically became a member of his or her mother's clan at birth. Clan membership could not be altered. The clans were vehicles for the provision of hospitality. One was obligated to protect fellow clansmen and to provide them with food and shelter (Fig. 3).

The clans were exogamous, i.e., members were required to marry outside of their clan. Members treated their clansmen as if they were parents or siblings, and sex within the clan was tantamount to incest. The preferred marriage partner was a real or classificatory cross-cousin

Fig. 1 Iroij (Chief) Joannes Peter and his wife Bela. Ujilang Atoll, Nov. 17, 1976. [Photo by Janet Lamberson.]

Fig. 2 Luther, an Enewetak elder and a repository of traditional cultural wisdom. Ujilang Atoll, Nov. 17, 1976. [Photo by Janet Lamberson.]

(father's sister's daughter or mother's brother's daughter), and a very high percentage of marital unions were of the preferred type.

Ideally, postmarital residence was patrilocal. A male took his bride to live on his father's land. Sometimes newlyweds lived with the man's parents, but the couple usually built a separate dwelling nearby. Quite commonly, a man and his married sons occupied adjacent dwellings but shared a common cooking house which was a separate structure. Thus, a patrilocal extended family was the most common family group located on a given *wato*.

Another facet of Enewetak Atoll culture that differed from that of the rest of the Marshalls was the system of land tenure and inheritance. In contrast to the rest of the Marshalls where matrilineages (subunits within the matriclans) constitute landholding corporations, the land tenure system at Enewetak Atoll was bilateral. In most cases, a married couple divided the land they had each inherited among their children, and a child usually received some land from both his or her father and mother. As the parental generation died and as members of the next generation married and produced children, the process was repeated with parents allocating land among their offspring (Fig. 4).

The people had an almost mystical attachment to their land, and their ties to it were deep. They could trace the history of their holdings back about a half-dozen generations. As indicated previously, an individual's identity was, at least in part, defined by one's *wato* and one's island of residence.

A final important social institution was an import. The people of Enewetak Atoll were the very last in the Marshalls to experience missionization because of their isolation and distance from the wetter, more richly endowed southern atolls where colonial powers always had their

Fig. 3 Aruo, a canoe builder and sailor, was lost at sea at Enewetak Atoll in 1983. [Photo was taken at Ujiland Atoll in 1977 by Janet Lamberson.]

headquarters. Not until 1927 did a Protestant missionary arrive to bring fundamental change to the people's world view. The first missionary was an islander from Mokil Atoll in the eastern Carolines, and he was followed by another missionary from Kosrae. The outsiders did not remain long, however, because within a few years a member of the *riEnewetak* community was trained to lead the spiritual life of the people.

The church took firm root. As in most places throughout the Pacific, the people fully embraced Christianity. Its teachings were mixed with traditional beliefs about ancestral and nature spirits and other notions about the supernatural, and the result was a hybrid that had become an integral part of the local culture and society. Work and play were tabu on Sundays. Other church services were held during the week. Christmas and Easter were the major holidays of the calendar year.

COLONIAL HISTORY

The Spanish explorer Alvaro de Saavedra is given credit for the European discovery of Enewetak Atoll in 1529. After his initial contact, like many other islands and atolls in the Marshalls and Carolines, Enewetak was not visited again by Europeans for many decades. The next known sighting of the atoll occurred in 1792, and 2 years later another European vessel called. In 1798, Enewetak Atoll was mapped by a Captain Fearn in command of the *Hunter* (Tobin, 1968). Although contact with the outside world surely has made some impression on the people, it seems somewhat odd that no accounts of early European visitors were found in the oral history of the people.

In 1898, shortly after the Germans had declared the Marshalls to be a Protectorate, a German trading company contracted the Enewetakese to extend their plantings of coconut palms for the copra trade. Some of the people traveled to Ujilang Atoll to work on the copra plantation there under a German supervisor. German rule was brief, however, and no German or other outsider actually took up residence on Enewetak during German times. In fact, the people were still adjusting to the European interlopers when Japanese colonial rule replaced that of the Germans in 1914 (Kiste, 1977).

Because they are much closer to Ponape Island in the eastern Carolines than the old colonial headquarters at Jaluit Atoll in the southern Marshalls, Enewetak and Ujilang Atolls were administered and visited by Japanese vessels from Ponape during Japanese rule. Consequently, the Enewetakese were separated even more from other Marshallese. It was also during Japanese times that the people lost some of their autonomy and lessened their control over their land. Japan began its rule with a show of force by sending naval vessels to confirm Japan's authority. In the early 1920s, a Japanese trader established himself on the atoll. He falsely claimed that the colonial government had granted him permission to acquire land and develop coconut groves. He also claimed that the people were required to assist him with the venture. Initially the Enewetakese did not resist and worked for modest rewards in trade goods, but as they became more familiar with the Japanese, they realized they had been duped, and the two chiefs filed a complaint with officials. The issue was not resolved before the Japanese military began to fortify the atoll in the late 1930s as part of the preparations that led to World War II.

The war years brought tragedy. First, the Japanese constructed an airstrip on Enjebi Island and evicted the *riEnjebi* to a small corner at the eastern end of their island. The American invasion in 1944 devastated and practically denuded both the Enjebi and Enewetak Islands. Ten percent of the local population was killed. At the end, both communities were moved to two small islands in the east side of the atoll. The Americans constructed a large military base on Enewetak Island, and the people acquired their third colonial master. When the Americans asked

Fig. 4 The Enewetak children represent the promise for the future. Ujilang Atoll, Nov. 17, 1976. [Photo by Janet Lamberson.]

them to abandon their homeland, the Enewetakese correctly concluded that they had no real alternative, so they offered no resistance (Kiste, 1977).

THE UJILANG RESETTLEMENT

Ujilang is 124 miles southwest of Enewetak. It had been inhabited by a Marshallese population, but in the late 1800s a typhoon decimated the atoll and killed all but a handful of its people, most of whom were moved to the southern Marshalls. Ujilang was then developed as a commercial copra plantation during the German and Japanese eras, and as noted, some of the people of Enewetak Atoll had experiences there as laborers during German times. Ujilang was abandoned during World War II, and thus it was available to receive a population.

American authorities initially thought of Ujilang as a site for the relocation of the Bikinians. They were the first to be moved to make way for the nuclear tests. Their first relocation occurred in March 1946 when they were moved to nearby Rongerik Atoll. It had never had a permanent population of any size, and the reason soon became apparent. Rongerik's resources, greatly overestimated by American planners, were inadequate to support the community. After considerable delay and many complications, the Americans decided to move the Bikinians to Ujilang, and in November 1947, an advance party of Bikini men and navy Seabees arrived to construct a village. In less than 2 weeks, however, officials in Washington, D. C. announced plans to use Enewetak as a second test site, necessitating a relocation of its inhabitants. They were moved to Ujilang on Dec. 21. The Bikinians were eventually resettled on small Kili Island in the southern Marshalls where they have never made a satisfactory adjustment (Kiste, 1974).

Ujilang has only one sizeable island, and both the *riEnewetak* and *riEnjebi* communities were resettled there. The island was evenly divided by an American naval officer who allotted one half to each community. A rather compact village was constructed in the middle of the island, with the Enewetak and Enjebi people residing on their respective sides of the dividing line. No longer separated by Enewetak's large lagoon and with the more compact settlement pattern, the two groups became a single community while retaining their dual political structure.

The years on Ujilang were quite difficult. The atoll is much smaller than Enewetak and has correspondingly fewer resources. Enewetak has 39 islands with a total land area of 2.75 square miles; its large lagoon covers 387.99 square miles. In contrast, Ujilang has 21 islands which collectively constitute only 0.67 square miles (Holmes and Narver, 1975; Tobin, 1968).

Compounding the problem of living on a smaller atoll with a greatly reduced resource base, the people, like other Micronesians, have rapidly increased in numbers. The total population at the time of relocation was only 141. By the early 1950s, the number had increased to about 170. By 1977, the population had reached 400 (Kiste, 1977). A census taken in 1978 reported 540 (Carucci, 1980), and today the number is probably in the vicinity of 600, a four-fold increase since relocation.

Population pressures on Ujilang's resources obviously increased during the people's years on the atoll, and on numerous occasions, food supplies from the land were depleted. Coconuts that might have been converted into copra were needed for sustenance, and as a consequence, the people had little cash to purchase imports. The situation was exacerbated because Ujilang is distant from the government center at Majuro, and ships carrying food and other supplies frequently failed to service the atoll. As a result, the people suffered considerable physical deprivation. For those who knew it well, memories of life at Enewetak brought despair, and younger people became convinced that they had been deprived of their true home where want was unknown. The desire to return to Enewetak increased with each passing year (Kiste, 1977).

In spite of the adversities suffered and the periods of discouragement, the people always maintained a great sense of pride in themselves and a determination to control as much of their destiny as possible. During the initial years of U. S. rule, the people sized up the Americans and attempted to determine the best ways of dealing with them. Until the mid-1960s, they tried to get help by making complaints and petitions to the administration. Welfare measures were occasionally implemented, but more often than not, the people's pleas went unheeded. During this period, the traditional political structure remained intact. The chiefs functioned in their usual roles, and as many traditional leaders elsewhere, they resisted American efforts to introduce Western political forms—in this instance, a council form of government headed by an elected magistrate. By the early 1960s, however, some change was observable. The two chiefs were by then older men. Some contemporary issues required that the decision-making processes be opened to include younger men who had attended American schools and/or had been employed by the administration. Meetings of adult males were occasionally held, and some decisions about community affairs were decided by a majority vote.

In 1967, exceptionally poor conditions on Ujilang and a realization that previous pleas to the administration had largely been ineffective prompted the people to take a much more aggressive stance. After an absence of 6 months, a field trip vessel called. Much to the surprise of the official in charge, the people boarded the ship and announced their intention to abandon the atoll. A potentially dangerous voyage on an overloaded ship was avoided when the officials volunteered to remain on the atoll and "suffer from starvation" until the administration responded to the situation. The display of assertiveness produced results. Substantial amounts of food and other supplies were soon delivered, and the District Administrator of the Marshalls came to hear the people's grievances.

The sit-in aboard ship and another threat to abandon Ujilang a year later had the greatest support from younger adults. The sit-in also seems to have been linked to a major transformation in the community's political structure. Sometime during late 1967, the two chiefs had yielded to younger men. A magistrate and a council of 12 were elected. Reflecting the traditional division of the population, the *riEnjebi* and the *riEnewetak* each elected six councilmen. The magistrate became the head of the entire community; the council became its legislative body. The chiefs, however, continued to function importantly as advisers and men of substantial influence (Kiste, 1977).

In 1968, the people evidenced considerable sophistication about the larger world when they petitioned the United Nations for assistance in returning to Enewetak. In August, it was learned that Bikini was judged to be safe from radiation and that it could be returned to its people.* The news caused great resentment among the *riEnjebi* and *riEnewetak*, and they strongly protested their continued alienation from home. The protest produced results. In 1970, in an effort to satisfy the people, the United States Congress authorized a payment of $1,020,000 to the people of Enewetak. Other payments were to follow in later years.

The initial attempt to placate the people was not successful. In late 1971, they announced their intention to return home before the end of the following year. Department of Defense (DOD) officials contended, however, that it was necessary for Enewetak to remain under DOD's control. This was rejected, and by early 1972, the people obtained legal counsel from the recently created Micronesian Legal Services Corporation (MLSC). The people then informed officials that they would institute legal action if Enewetak was not returned to them. On April 18, 1972, the long-awaited day arrived; it was announced that the U. S. would surrender Enewetak by the end of 1973 after certain "unspecified activities" had been completed there.

The people had won a major victory, but it soon became apparent that the "unspecified activities" were a threat to their future well-being. The activities were part of

*In 1968–69 a cleanup was conducted at Bikini Atoll, and a residential complex was established. About 140 Bikini people returned to Bikini in the early 1970s, but by 1978 it became apparent that the radiation content of foods grown at Bikini made permanent residence there inadvisable. The Bikinians were again removed from their atoll and, at this writing, have not yet returned.

the Pacific Cratering Experiments (PACE) project and were sponsored by the DOD and related agencies. PACE had commenced with small explosions and was projected to culminate in several multiple ton detonations of high explosives and one final 500-ton blast. It was hoped that this series of experiments would help to provide a better understanding of many of the effects of the tests of the 1950s. The people of Enewetak, represented by their MLSC lawyers, invoked the provisions of the National Environmental Policy Act, and they filed suit in the Federal District Court in Honolulu in September. At Ujilang, PACE scientists explained their project, claiming that it would cause no long-term damages. The people listened politely and responded with a brief but very firm statement. In essence, they stated: "PACE is evil, and we will do whatever we can to prevent it." The magistrate gave an eloquent speech which reflected the people's values and feelings.

> I do not know if you have made an attempt to compare your sense of values, you who live in America or elsewhere, with ours. You live with gold and money and we have to depend on land and whatever life we can find on land and in the water. Without these, we are nothing. We do not have to explain further that Enewetak, with whatever land resources and whatever marine resources it has, is our homeland, and seeing that you understand this, we do not know why you continue to insist to do these things on Enewetak, when for us there is really nothing else to look forward to. For this reason we must continue to ask that you refrain from proceeding with this program. PACE is no good . . . Enewetak has undergone severe damage. There are islands that are missing. There is a considerable amount of land that has been destroyed. The question then comes: Has not Enewetak done enough for your testing? We do not know who you will take this message to—perhaps you will take it to Washington or the Department of Defense—but, the point still remains that we feel

Fig. 5 Official ceremony returning Enewetak Atoll to its former inhabitants, Enewetak Atoll, Sept. 16, 1976. From left to right, seated at the table, are Oscar DeBurum, then District Administrator of the Marshall Islands; Binton Abraham, Iroij (Chief) of the *riEnewetak*, now deceased; Thomas Lacy, Brigadier General, U. S. Air Force, then Field Commander, Defense Nuclear Agency; Peter Tali Coleman, then Deputy High Commissioner of the Trust Territory of the Pacific and later Governor of American Samoa; Joannes Peter, Iroij (Chief) of the *riEnewetak*; Hertes John, magistrate of Ujilang Atoll. [Photo by Janet Lamberson.]

> that Enewetak has done enough. We have sacrificed enough and PACE should not be continued because it only means further destruction of our homeland. [Office of the Judge Advocate Pacific Air Forces, 1973.]

The legal suit was never brought to trial as the DOD cancelled the PACE project soon after the public hearings (Kiste, 1976).

That the magistrate and not the chiefs spoke for the people reflected the changes that had occurred in their political organization. By the time of the PACE affair, further change had occurred because the process of electing councilmen had been altered. In elections subsequent to 1967, the 12 councilmen were elected from the population at large and not half from the Enewetak and half from the Enjebi sides of the community. It appeared that the old division between the two sides had lost some of its meaning.

RETURN TO ENEWETAK

After the PACE affair, the people experienced some reversals. Radiological surveys revealed that some islands of Enewetak Atoll are more heavily contaminated by radioactive debris than previously thought, and they cannot be inhabited for decades to come. In 1976, after extensive radiological surveys, it was determined that Enewetak Island and several others on the atoll's eastern rim could be partially restored with reasonable safety. The U. S. Congress provided funds for their cleanup and rehabilitation. The full-scale cleanup effort began in late 1977. The Enewetakese were consulted in the planning and some were employed to help with the work. The cleanup of Enewetak Atoll, the construction of dwellings and community buildings, and extensive replanting was completed in 1979, and the atoll was officially returned to the people in April 1980 (Figs. 5 and 6). The event was celebrated by virtually the entire population with 542 people attending.

Fig. 6 Iroij Joannes Peter signing documents returning Enewetak Atoll to the *riEnewetak* and *riEngebi*, Enewetak Atoll, September 16, 1976. [Photo by Janet Lamberson.]

OTHER ISSUES

Although the Enewetak case is unique, the people share some historical trends with other Micronesians. Like other islanders, the people of Enewetak have had to become familiar with the representatives of the successive colonial administrations. The Enewetakese had to learn the customs of the new foreigners and had to develop ways to cope with them.

The initial years of American rule followed on the footsteps of World War II, and it was a time when memories were still fresh of the destructive powers that the U. S. had unleashed during its crushing defeat of Japan in the Pacific. Understandably, Micronesians were cautious and even timid in their dealings with Americans.

With the passing of time, Micronesians everywhere grew bolder and became more skilled as they managed their relations with Americans. Encouraged by this relationship, Micronesians have modified their traditional institutions and have adopted more democratic political structures. In recent years, and very much like the people of Enewetak, they have become more assertive as they have negotiated for what they believe are their own best interests. Inspired by the general wave of decolonization in the Pacific, and as the end of the U. S. trusteeship draws near, Micronesians have been struggling to take control of their own lands and destinies. Self-government is coming to the U. S. territory, and it seems unlikely that situations such as those which occurred at Enewetak or Bikini will ever occur again.

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Chapter 3

Physiography of Enewetak Atoll

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LOCATION AND SIZE

Coral atolls have been variously defined and, without considering unusual cases, can be described as more or less continuous reef (largely corals and other calcium carbonate producing organisms), which surrounds a deeper lagoon and drops steeply to oceanic depths on the seaward margin. All islands are typically low, derived from reef rubble and sand. Enewetak Atoll conforms to all aspects of this description and in many respects is a "textbook" atoll. It has a large elliptical lagoon, approximately 41 islands on its rim, a few passages between the lagoon and ocean, and narrow shelves dropping steeply into deep water on all sides. The subsurface geology of Enewetak and Bikini have been extensively examined, and these results are reported in the *U. S. Geological Survey Professional Papers 260* series.

Enewetak Atoll is located in the northwestern Marshall Islands with its center at approximately 11°30'N; 162°15'E (Fig. 1). It is 220 km from the nearest land, Ujelang Atoll to the southwest; 310 km from Bikini Atoll to the east; and about 410 to 460 km from other atolls (Ujae, Wotho, Ailinginae, Rongelap) to the southeast to east. To the north occur Wake Island, about 1000 km northeast, and Marcus (Tora Shima) Island, about 1600 km northwest. To the west are the Marianas, the nearest being about 1700 km. All islands of the Marshall Islands are low, most being coral atolls. The high islands nearest to Enewetak are Ponape, to the southwest, and Kusaie, to the south, both about 580 km distant.

Enewetak is a relatively large atoll, somewhat elliptical in shape, about 33 by 41 km in size, with the islands, reef flat, and lagoon covering about 1000 km^2. It is the third largest atoll in the Marshall Islands, exceeded by Kwajalein (the largest atoll in the world) and Rongelap. By worldwide standards, it is not exceptionally large. The majority of the area of Enewetak is the lagoon, with the reef flat and the islands covering progressively less area. Table 1 provides information on the area covered by various environments at Enewetak.

WEATHER AND CLIMATE

Weather at Enewetak is dominated by the surrounding marine conditions. Since all islands are low and of small area, they do not alter weather conditions by their presence. The atoll is semiarid, with rainfall averaging only about 1700 mm per year, and has a distinct wet–dry annual cycle. Air temperatures are relatively high and very stable, with a mean annual temperature of about 28°C. Solar radiation is intense, and humidity is consistently high.

At almost 12°N, Enewetak is within the trade wind belt with nearly consistent easterly winds. The atoll is subject to tropical storms and typhoons at irregular intervals which greatly affect the marine and terrestrial environments. The meteorology of Enewetak is discussed in Chapter 6 of this volume.

ENVIRONMENTS OF ENEWETAK

The Lagoon

The lagoon is the largest component of the atoll. It is relatively deep by atoll standards, averaging about 54 m, with a reported maximum of 71 m. The lagoon bottom generally slopes from the lagoon rim toward the center. At a distance of 2 to 4 km from the rim, the lagoon bottom is essentially flat at a depth of about 45 m. Even the outermost 2 to 4 km of the lagoon has generally low slope gradients on its bottom because of the horizontal distance required to reach 45 m depth. The only areas with significant slopes, except along the flanks of patch reefs and coral pinnacles, on the soft bottom of the lagoon occur shallower than 25 m. Below that depth, except for small-scale undulations, there is little variation in the soft bottom from the flat and horizontal. The area above 25 m depth is also affected by wave action and currents which can affect sediment distribution.

Most of the lagoon bottom is relatively inaccessible to human observers. The depths are below those practical for sustained diving operations and, generally, must be observed or sampled remotely. The area of the lagoon bot-

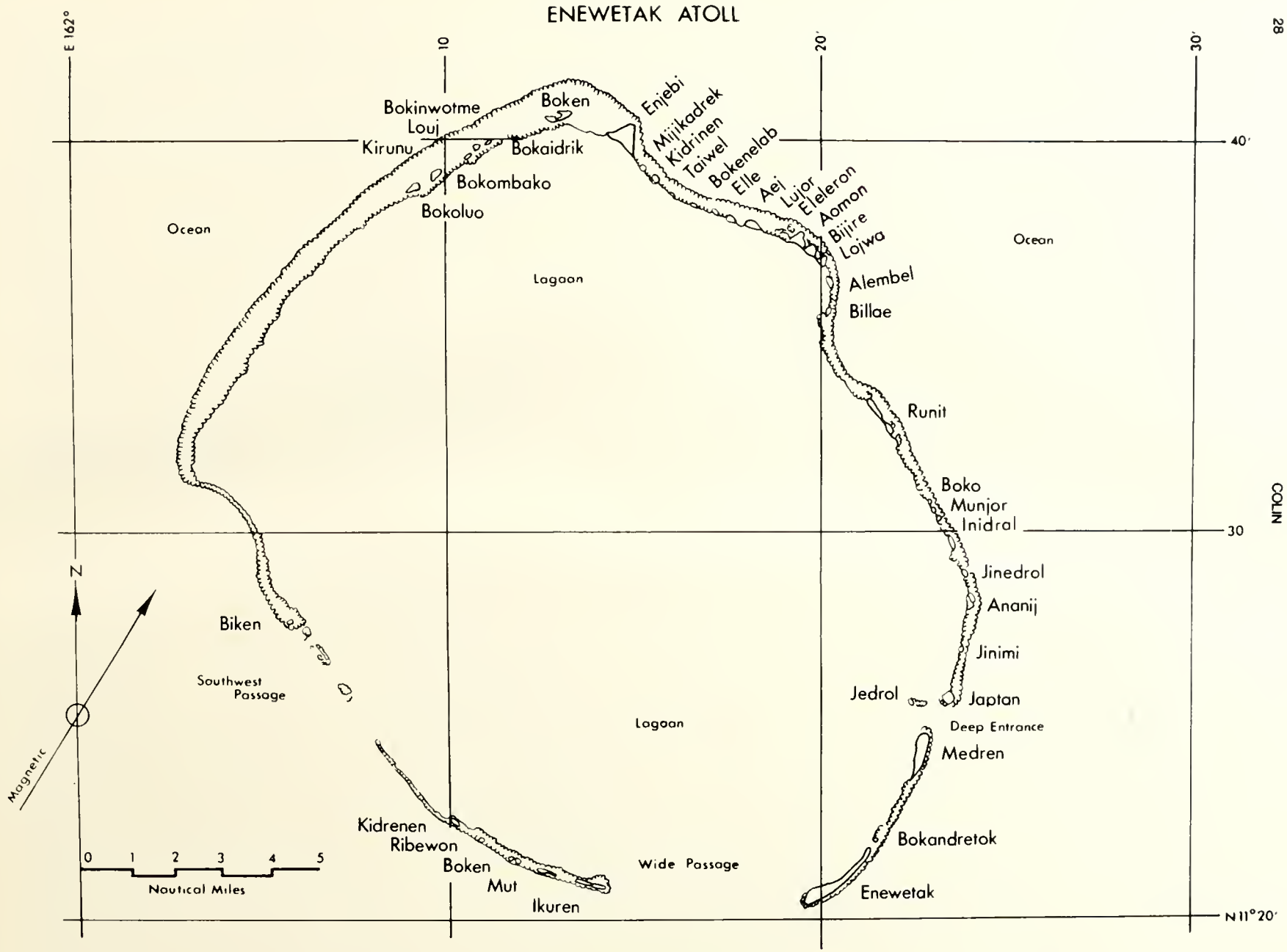

Fig. 1 Map of Enewetak Atoll.

TABLE 1

Areas of Environments at Enewetak Atoll (in kilometers)

Total atoll (land and shallow water less than 100 m deep)	1022	
Total land		7.125
Total marine environment	1015	
Total lagoon depth in meters	938	
0 to 10	47	
10 to 20	56	
20 to 30	75	
30 to 40	103	
40 to 50	253	
50 to 60	310	
Over 60	94	
Outer reef slope	est. 13	
Reef flat (less than 1 m at low tide)	64	

tom visible in aerial photographs is limited to depths of 15 to 20 m and is usually located only on the rim of the lagoon. The only structures which are visible from the surface in the central lagoon are coral pinnacles which reach within less than 15 to 20 m of the surface.

There are two major channels between the lagoon and ocean (Figs. 2 and 3). The first is the "deep" channel, between Medren and Japtan, which is nearly 60 m deep in places but is relatively narrow. It averages only about 1.4 km in width between Japtan and Medren, but the deepest portion (below 40 m depth) is only about 600 m wide. During tidal changes, swift currents flow in and out of this channel. It is exposed to the easterly swell from the ocean and allows such swell to enter the lagoon in its vicinity. The swell, combined with wind-produced chop due to the open fetch of the channel and currents flowing out of the lagoon (counter to the wind direction), often produces extremely rough conditions in the channel.

The deep channel splits into two branches just west of Jedrol Island leaving an area of shallow reef in between with minimum water depths of about 6 m (Fig. 2). This wedge-shaped reef gradually deepens both to the west and north until it essentially merges with the lagoon bottom. Near its easternmost extremity, a ferro-cement barge—the "Concrete No. 9," locally called the "cement ship"—ran aground, resulting in a distinctive marker of this site. The bottom slopes away at about a 45° angle into the branches of the deep channel which begin to flatten out at about 40 m depth.

The second major passage, the "wide" channel, is located at the south end of the atoll between Enewetak and Ikuren. It is no more than 15 to 18 m deep but stretches 10 km between the islands (Fig. 3). Since it is considerably shallower than the deep lagoon bottom, it resembles a sill. The currents in its vicinity are essentially unidirectional, out of the lagoon (Atkinson et al., 1981), but their speed is determined by the tide. Although the wide passage does not directly face the ocean swells, the swells are refracted somewhat around the southern end of Enewetak Island and enter the lagoon through this opening. This, combined with waves from the lagoon and the

Fig. 2 Aerial view of the deep, narrow channel entrance to the lagoon between Medren and Japtan Islands on the eastern, windward side of the atoll. [Photo by P. L. Colin.]

Fig. 3 Aerial view of the wide, south channel passage to the lagoon looking from Enewetak Island (lower right) to Ikuren Island (upper left). The shallow bottom of the sill at the passage is visible. [Photo by P. L. Colin.]

shoaling nature of the bottom at the wide passage, produces rough conditions with standing waves and steep waves in the western half of the wide passage.

A series of shallow open passes with fingers of emergent to near emergent reef interspersed between them is called the "southwest passage," an additional passage between the lagoon and ocean. These openings cover about 6.7 km of the atoll margin from the island of Biken to the beginning of unbroken shallow reef to the southeast. The sand-bottomed passes appear deeper to the south—as much as 8 m deep in places. While significant, the southwest passage is perhaps an order of magnitude less important in lagoon–ocean water transport than the deep and wide channels (Chapter 5 of this volume).

The reef flat is also a major source of water movement into or out of the lagoon. The amount of such transport is dependent on the height of the tide and the wind and waves which influence the wave pumping of water from ocean to lagoon. Where islands disrupt the free flow of water across the reef flat into the lagoon, water flow is channeled into narrow, deeper areas where current speed can be relatively high. These channels are variously termed "rips" or "gutters" and can also occur on intraisland reef flats where there are areas of higher current flow.

The biological communities and environments of the lagoon are discussed in Chapters 7 and 8 of this volume. They are quite variable from place to place, varying from sediment-bottomed areas devoid of hard substratum to well-developed coral reefs. The diversity of plants and animals is as high in the lagoon as it is in other areas of the marine environment.

Emery et al. (1954) reported over 2000 "coral knolls" in the lagoon with some suggestion that they "belong to 2 distinct size categories; nearly all the large coral knolls have a diameter in excess of 1 mi whereas nearly all the rest are smaller than ⅓ mi, and intermediate sizes are not common." Most of these do not reach sufficiently close to the surface to be visible and can be detected only by echo sounding. Emery et al. (1954) distinguished between the term "coral pinnacle" and "coral knoll," preferring the latter term, but did not clarify how the reef structures of the lagoon margin were considered. In essence an intergrading series of reef structures exists within the lagoon. Although distinct types—such as coral knolls (broad, relatively low structures), coral pinnacles (high relief relative to diameter), and patch reefs (small structures, often in shallow water)—can be identified, intermediates are common. Those reef structures that are present on the bottom and visible from the air are generally, in this treatment, considered to be "patch reefs."

The Reef Flat

The shallow reef flat, much of which is emergent at low tides, around the rim of the atoll has been the most intensively examined marine environment. It consists of areas of rock pavement with seaward algal ridge structures and lagoonward rubbly bottom. The reef flat varies considerably in different areas of the atoll, particularly between the windward and leeward sides but also over relatively short distances on the windward shore. Very little of the algal ridge, normally produced by coralline algae, is "live" at Enewetak. Instead of the healthy pink corraline areas

which have the characteristics of typical algal ridge structures, they are covered with fleshy algae. Indications are that these areas were live algal ridges sometime within the relatively recent past, but whether man has played a role in their demise is uncertain. There is one small area of live algal ridge still present at Enewetak, near the island of Ananij, which occurs at the easternmost extension of the reef flat. This and the ecology of the reef flat are discussed in subsequent chapters.

The Seaward Slope

The seaward slope from the reef flat to the dropoffs to depths over hundreds of meters is narrow all around Enewetak. The edge of the seaward slope is marked by "spur and groove," alternating reef and rubble fingers projecting seaward where the waves break. On leeward reefs, there are no distinct spur and groove formations but a deeper series of promentories and reentrants in the upper 15 m. On windward reefs, a rock bottom then slopes away gradually to a break point at the 18 to 30 m depth where the bottom begins to slope much more steeply. Oceanic depths are quickly reached.

The width of the seaward shelf varies around the atoll. It is widest off Enewetak Island, being about 400 m wide. Other areas of the windward reefs are narrower so that it is only 100 to 200 m wide on the northeastern reefs between Lojwa and Enjebi. On leeward shores the shelf is very narrow, only a few tens of meters wide. It is literally possible to stand on the reef flat and throw a stone into depths of 100 fathoms.

The Islands

There are approximately 40 islands at Enewetak, excluding a few small sand islands remaining above water at high tide. Two islands (Elugelab and Lidilbut, not shown in Fig. 1) were vaporized by nuclear testing, and three others were so severely altered that only small remnants remain (located in the northwest part of the atoll). The vegetation of most islands at Enewetak has been progressively and increasingly altered compared to the nondisturbed state. The alterations occurred initially by the establishment of coconut groves, later by wartime construction and damage, and finally by nuclear testing activities and subsequent military activity. Extreme alteration occurred again during the Enewetak cleanup with the aim of reestablishing the coconut groves. The only islands which have essentially undisturbed vegetation are the five southwestern islands and Biken (see Chapter 11 of this volume and Chapter 3 of Volume II for further details).

The islands can be grouped into several reasonably natural units defined by significant gaps between units and identified by direction location. Often these units are identified by compass location and are defined here.

The "southwest islands" of Enewetak are the five islands from the southerly Kidrenen through Ikuren. They are separated by both distance and intervening passes from isolate Biken, which will be termed the "western island," and from Enewetak Island. The islands of Enewetak, Bokandretok, and Medren are called "southeastern islands"; they share a common reef flat and are separated from all others by passes. The ten "central islands" are those of the windward side from Japtan through Runit, including Jedrol. The "northern islands" are those 15 to 16 islands from Bijire or Billae through the northern Boken. They are separated from the central islands by several kilometers of open reef flat. The last group, the "northwest islands," from Bokoluo to Luoj, are separated from the northern islands by the large MIKE and KOA craters and consist of four islands and one sand bar.

The islands consist largely of coral sand, rubble, and boulders with areas of exposed beach rock and reef flat pavement. In certain areas, large quantities of cement debris are incorporated among coral boulders and rubble. All the islands are low, the highest elevation being approximately 4 m on Enewetak Island. Beaches occur on many lagoon shores, the most extensive and continuous today found on Medren. Enewetak Island in pretesting days possessed an apparently continuous beach, but the lagoon shore has been so altered by the construction of seawalls or by the dumping of riprap that sand beaches occur only in short stretches today.

The ocean shore of islands on the windward side of the atoll facing the reef flat often have alternating beach–beach-rock shores. Sand beaches here, however, do not extend below the intertidal, merging with the reef flat or rock which extends offshore.

Vegetation occurs above the high tide line on all shores. There are no mangroves or mangrove-like terrestrial plants extending into salt water at Enewetak. With the exception of Biken and the five southwestern islands, the vegetation has been extremely altered.

Enewetak, Medren, and Japtan Islands are residence islands. Houses were constructed and other buildings were converted during the Enewetak cleanup. These three residence islands, plus Ananij and the islands from Billae through Aej, were planted with coconut palms between 1978 and 1979. Coconut palms have not been planted on Enjebi, the second largest island of the atoll, except for an experimental garden plot that was established in 1975 by Lawrence Livermore National Laboratory and that contains coconuts, pandanus, and breadfruit.

The soil of Enewetak Atoll islands consists of little more than calcium carbonate sand and rubble (Chapter 11 of this volume). This material has virtually all its origin from the sea and is derived from corals, calcareous algae, foraminifera, and a wide variety of organisms producing smaller amounts of carbonate materials. Occasionally, pieces of pumice which have drifted to Enewetak are found near beaches. More rarely, noncarbonate rocks, carried by rafting debris such as fallen trees, are found.

Enewetak soils have very little organic matter or nutrients. This is particularly true for the highly disturbed islands where human activity has eliminated the normal ground cover of vegetation and nesting birds. On normally vegetated islands, a limited amount of organic material is

tied up in leaf-litter on the soil surface, but relatively little is actually found in the soil.

The larger islands of the atoll have good freshwater lenses beneath them. All the islands are quite low, so the water table lies very close to the ground's surface. It is not necessary to drill more than about 3 m deep to hit water. The groundwaters of Enewetak have been studied in some detail (Chapter 4 of this volume).

MAN-MADE FEATURES

Quarries

Areas of reef flat adjacent to several islands at Enewetak were quarried or excavated for building or road construction purposes. A single quarried area is at the north end of Enewetak Island adjacent to MPRL (Fig. 4). This area was quarried during the Japanese occupation. Because a wide area of reef flat was left seaward to reduce wave swell entering the quarry, the Enewetak quarry is calm during low tides and is an ideal location for snorkling and diving. Numerous investigators at Enewetak have taken advantage of this. The Enewetak quarry covers about 2.75 hectares and averages about 1.5 m in depth, with the deepest spot being 3 m. The biological communities present in it are discussed in Chapters 7 and 8 of this volume.

The reef flat at the south end of Medren Island was also quarried. Although slightly larger than the Enewetak quarry, little protective reef flat was left seaward of it; therefore, it is more open to wave action from the open ocean. A small quarry occurs at the north end of Medren on the reef flat.

Seven relatively small areas were quarried on the reef flat near the middle portion of Runit Island. All are well inside the seaward margin of the reef flat and are well protected from waves at low tides.

At Enjebi, there are a few areas toward the north end where the reef flat was quarried. There is one elongate rectangular quarry and two small round ones. Also, on the western side of the island are three irregular areas next to shore, deeper than the adjacent bottom, which were probably quarried for construction of the Japanese airstrip there during World War II.

Craters

Six craters remain from nuclear weapons testing at Enewetak. Three craters are the result of atomic bomb tests. The other three are from thermonuclear weapons tests and are roughly three orders of magnitude larger in area and volume. Two atomic bomb craters are at the north end of Runit Island (Fig. 5). The histories, morphology, and subsurface geology of the Enewetak craters are extensively discussed by Ristvet (1978), resulting from work done by the Air Force Weapons Laboratory, Albuquerque. Both Runit craters are about 120 m in diameter. The most lagoonward, Cactus crater, was used for construction of the Cactus crater crypt during the Enewetak cleanup from 1977 through 1979 in which the crater was filled with cement, contaminated debris, and soil. A

Fig. 4 Aerial view of the north end of Enewetak Island showing the buildings of the Mid-Pacific Research Laboratory and to the right of them the quarry on the reef flat. [Photo by E. S. Reese.]

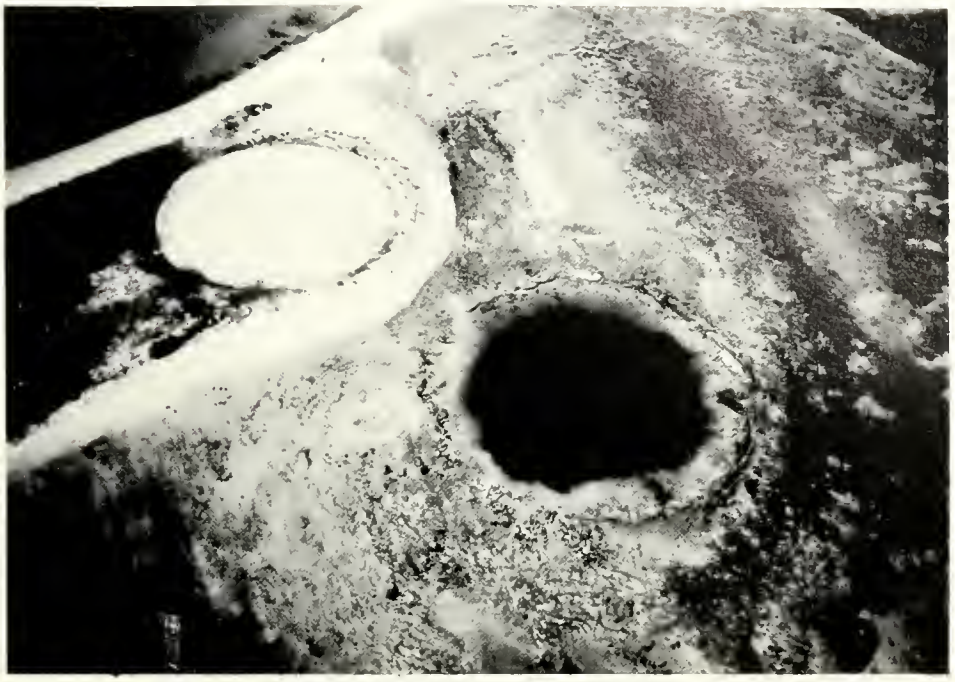

Fig. 5 The north end of Runit Island with La Crosse crater (lower right) and the Cactus Crater Crypt (upper left). La Crosse crater is about 120 m across and about 10 m deep. The Cactus Crater Crypt was built in the crater to contain contaminated soil and debris. [Photo by P. L. Colin.]

Fig. 6 The island of Boken (north) with the Seminole crater, a small atomic bomb crater. The island and adjacent islands in the foreground have been drastically altered by the formation of the crater. [Photo by P. L. Colin.]

25-foot-high cap of poured cement plates covers the crypt. The seaward crater, Lacrosse crater, was not altered during construction of the Cactus crypt. Nolan et al. (1975) described the distribution of substrate types in these craters and fish assemblages occurring in them (Chapter 7 of this volume).

The third atomic crater is on the west side of Boken Island in the north of Enewetak (Fig. 6). It is similar in size to the Runit craters, roughly 200 m in diameter, 10 m deep, and is connected to the sea via the reef flat.

Two of the thermonuclear craters are located between Boken and Bocinwotme Islands (Fig. 7). The MIKE crater is the western one, roughly 1.8 km in diameter and 56 m deep. The KOA crater to the east is slightly smaller, about 1.5 km in diameter. Both blasts were detonated on islands which disappeared with formation of the craters. A third island, Bogairikk (not shown in Fig. 1), was largely eliminated with formation of the craters and is now represented solely by remnants on the sandbar west of Boken. The MIKE crater breaches the shallow reef into the lagoon at the 10 to 15 m depth contour. The KOA crater is still separated from the actual lagoon by a shallow bottom of less than 6 to 10 m depth but is confluent with the MIKE crater on its west side. A minimum of about 400 m of reef flat separated the MIKE crater from the open ocean; a slightly greater margin exists between the ocean and KOA crater.

The last crater is some 7 km southwest of Bokoluo, the westernmost of the northern islands. The device was exploded from a boat anchored over the shallow lagoon margin. This produced a crater which excavated northwestward in the shallow reef and reef flat but is very open to the lagoon to the southwest. It is roughly 1.7 km in diameter.

Other Physiographic Effects from Nuclear Tests

A large area of reef flat and seaward reef face cleaved away in the area north of the MIKE crater sometime between 1952 and 1958 (Fig. 7). The section of reef did not break away as a result of the MIKE test but was split off sometime later. About 300 m of the reef face, running as much as 60 m inward on the reef flat, fell away, and there is no bottom visible in aerial photos over what was once reef flat. This represents an exposure of underlying reef structure which is of unprecedented magnitude (see Chapter 4 of this volume for details). Direct examination of this scarp reveals that it is vertical to slightly overhanging with relatively sparse benthic organisms on its upper surface.

Other nuclear-produced phenomena still visible at Enewetak include ejecta trails on the reef flat produced by thermonuclear tests, particularly in the area of the craters,

Fig. 7 Mike (right) and KOA thermonuclear craters on the northern reef at Enewetak Atoll, photographed from 10,000 feet. The larger Mike crater is about 1.6 km across. The island of Boken with the small Seminole crater is seen on the left side of the photograph. The section of outer reef face which cleaved off after the KOA test can be seen seaward of the Mike crater at the bottom of the photograph. [Photo by P. L. Colin.]

plus small depressions on the reef flat probably produced by single ejecta blocks.

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Chapter 4

Geology and Geohydrology of Enewetak Atoll

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INTRODUCTION

Enewetak Atoll is located at 162° east longitude and 11° north latitude in the Pacific Ocean. It is the northwesternmost member of the western Ralik (Sunset) Chain of the Marshall Islands. Enewetak Atoll is one of the larger atolls; it is roughly elliptical in shape, with a north–south length of 40 km and an east–west width of 32 km (Fig. 1). The reef is cut by three passes. The Deep Channel on the southeast side is only 1.5 km wide, but it has a depth of 55 m between Japtan and Medren Islands. The South Channel is approximately 9.5 km wide but is only 10 to 20 m deep. The Southwest Passage is even shallower, only 2 to 4 m in depth. Maximum tidal currents of nearly 1 m s^{-1} in the Deep Channel and 0.5 m s^{-1} in the South Channel have been observed (Emery et al., 1954). The reef may be divided into four parts with distinct morphologies related to their positions relative to the prevailing northeast trade winds. The parts are the windward reef on the northeast, the leeward reef on the southwest, and the two transitional reefs on the northwest and southeast (Fig. 1). The reef encloses a lagoon of 920 km^2 with a maximum depth of 65 m. The lagoon has a relatively smooth carbonate sediment bottom studded with hundreds of coral pinnacle and patch reefs (Emery et al., 1954). Forty-two low-relief islands and islets composed of carbonate sands and gravels exist on the atoll with a total dry land area of 6.7 km^2 with the largest islands being about 1 km^2 in area.

Enewetak Atoll receives an average annual rainfall of 1470 mm, mostly during August to December. Rainfall is highly variable with annual totals ranging from 605 to 2422 mm (Buddemeier, 1981). Tides are of the mixed semidiurnal type with a maximum range of about 1.8 m.

The purpose of this chapter is to summarize the vast wealth of data on the geological aspects of Enewetak gathered over the last 40 years.

A SUMMARY OF GEOLOGIC INVESTIGATIONS

The history of investigations of atoll geology in general and Enewetak Atoll in particular may be divided into three periods: pre-1946, 1946 to 1964, and post-1964. The first period was one of discovery and initial exploration. These early observations became the framework for many hypotheses on the origin and evolution of atolls. Most of the early studies focused on the surficial geologic features and lacked the direct sampling of subsurface data to evaluate the many hypotheses of the day. Beginning in 1946, there was a significant increase in knowledge of atolls resulting from a series of comprehensive scientific studies of the northern atolls of the Marshall Islands, particularly Bikini and Enewetak. These geologic investigations were conducted by U. S. Geological Survey (USGS) scientists for the U. S. Atomic Energy Commission (AEC) to establish baselines to assess effects from nuclear weapons testing conducted at Enewetak and Bikini between 1946 and 1958. A vast amount of surface and subsurface geologic data was gathered and analyzed, and the results were published through 1964 (cf. Emery et al., 1954; Schlanger, 1963). From 1964 to the present, scientific studies have been of two types: those which have continued to address the problems conceptualized by earlier studies and those which have addressed the effects of the nuclear weapons testing at the two atolls. Enewetak Atoll continues to this day as one of the sites of significant studies of atoll geology, carbonate sedimentology, and organism/sediment interrelationships.

Pre-1946 Period

The first geologic studies of the Marshall Islands were conducted in 1816 and 1817 by Albert Chamisso. Chamisso, a naturalist with the Russian Von Kotzebue expedition to the northern and western Pacific Ocean, described the reefs, islands, and lagoons of the eastern chain of the Marshalls. For the rest of the 19th century the Marshalls were visited only by general surveying expeditions (Emery et al., 1954).

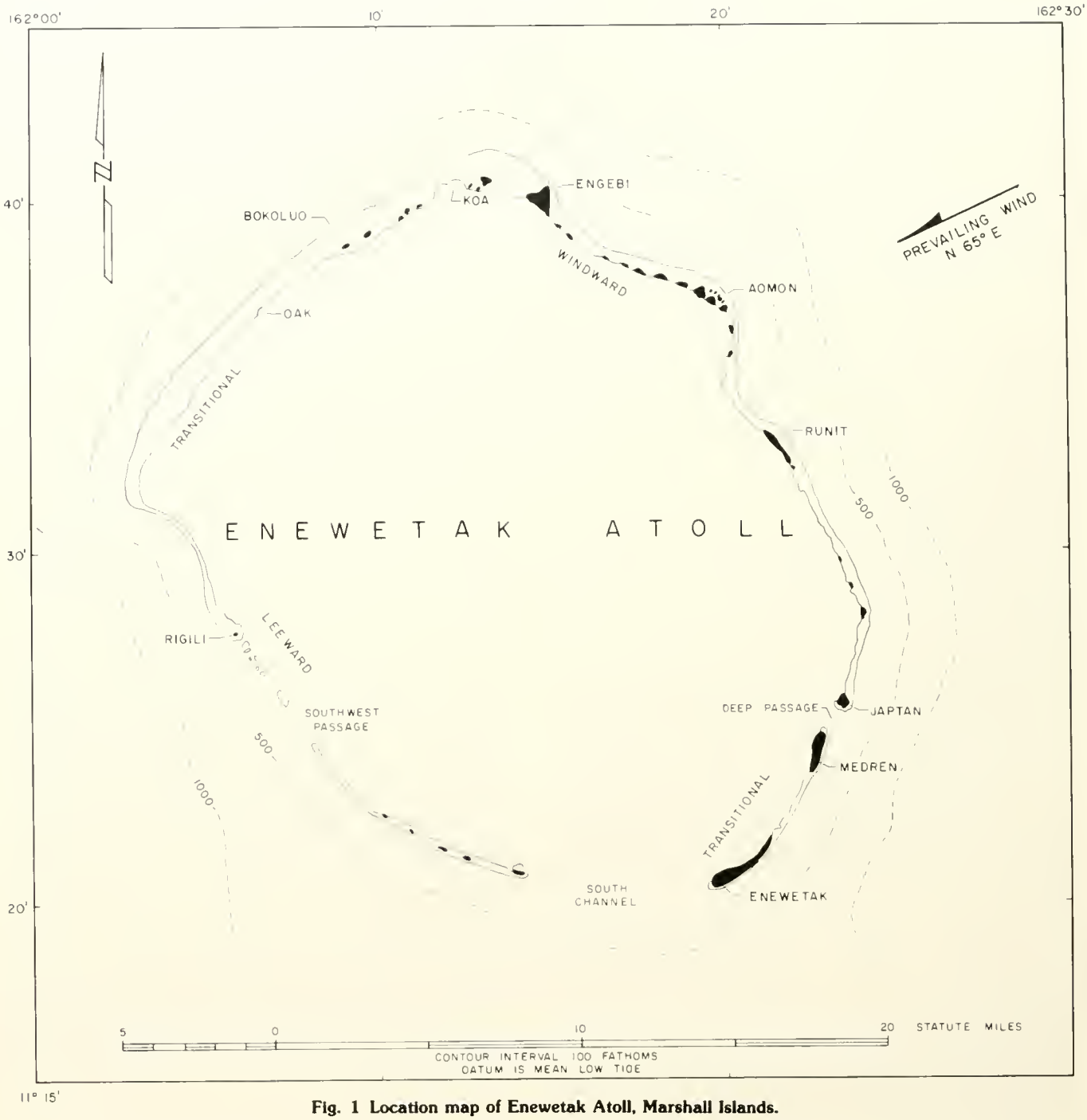

Fig. 1 Location map of Enewetak Atoll, Marshall Islands.

Meanwhile, expeditions in other areas of the world were contributing to an understanding of atoll geology. Darwin (1842), during the voyage of the HMS *Beagle* from 1831 to 1836, studied reef building organisms and reef morphologies. He established a three-fold classification of reefs that is still used today: fringing reefs, barrier reefs, and atolls. Darwin (1842) integrated his findings into a theory of atoll formation on subsiding island foundations with antecedent fringing and barrier reef stages. However, other workers (cf. Agassiz, 1903; Daly, 1915; and Gardiner, 1931) later proposed alternate theories postulating that atoll reefs grew upwards from still standing submarine summits of various origins.

By the turn of the century, direct subsurface sampling became a paramount issue to understanding the origin of atolls. Funafuti Atoll, in the Ellice Islands 2400 km south

of Enewetak Atoll, was the site of the first sampling well drilled on an atoll (David et al., 1904). This well, drilled from a ship in the lagoon, penetrated 337 m of carbonate sediments, demonstrating the great thickness of atoll reef sediments.

A major review of the theories of atoll formation was written by Davis (1928). Davis carefully evaluated the data and hypotheses; his evaluation supported Darwin's (1842) subsidence theory as correct and rebutted alternate theories. Although Davis (1928) rejected Daly's (1915) theory that glacial period sea level histories resulted in atoll formation, he did enter them as an important new element to consider in evaluating the geologic history of atolls.

Before 1946, atolls of the Marshall Islands provided little evidence for the aforementioned theories. During the period of 1918 to 1944, the Marshalls were under the control of Japan; although Japanese scientists conducted studies on the atolls, much of the resulting data are not readily available (Emery et al., 1954). Stearns (1945) made some general comments on possible battle damage to the reef of Enewetak Atoll following the American occupation in 1944.

In summary, at the end of 1945, only a small body of data existed on atoll geology. The general locations and morphologies were described, and the types of reef-building organisms and their environmental requirements were known in a general sense. Conclusive evidence on atoll formation had not been found, and sparse data existed on subjects such as atoll foundations, ages, lagoon and outer slope sediments, reef zonations and productivities, and ecology.

1946 to 1964 Period

A period of intense scientific study on the northern Marshall Islands began in 1946 to establish baselines from which damage could be assessed from the U. S. Nuclear Weapons Testing Program. Bikini Atoll was chosen to be the site of the first nuclear weapons effects tests conducted by the United States. Operation Crossroads, consisting of the detonation of two atomic bombs over and under naval ships in Bikini Lagoon, was conducted in 1946. Two expeditions to Bikini were made in 1946 and 1947 to study the atoll environment. The 1946 effort included general surficial geologic studies of the reef, lagoon floor and outer slopes, and a seismic refraction study of the subsurface structure of the atoll (Emery et al., 1954). The 1947 studies yielded much geologic information on the subsurface through the drilling of three holes on Bikini Island and reef, with one hole penetrating 775 m of carbonate sediments (Ladd et al., 1948). In 1950 additional seismic refraction studies were completed at Bikini and the adjacent Sylvania Guyot and the southern part of Kwajalein Lagoon (Dobrin and Perkins, 1954; Raitt, 1954). An aeromagnetic survey of Bikini Atoll (Keller, 1954) was also completed.

Nuclear testing began at Enewetak Atoll in 1948 with three events of Operation Sandstone. Shortly thereafter, the USGS began a series of geological and scientific investigations again to establish baselines to measure the effects of the nuclear detonations. In 1950 four shallow holes were drilled by the AEC in the reef on the seaward side of Engebi (Enjebi) Island to locate a suitable rock quarry (Ladd and Schlanger, 1960). In 1951 the AEC drilled 17 shallow holes on six different islands for soils engineering studies related to the construction of structures for the nuclear testing. The AEC also drilled three deep holes on the atoll in 1951 and 1952 under the technical guidance of the USGS: K–1B was drilled to 390 m on Engebi (Enjebi), F–1 was drilled to 1411 m on Elugelab, and E–1 was drilled to 1287 m on Medren Island. Both F–1 and E–1 reached volcanic basement with 5 m of olivine basalt being recovered from E–1. The confirmation of a basaltic foundation beneath Enewetak Atoll substantiated Darwin's subsidence theory of atoll formation (Ladd et al., 1953). Drill holes K–1B and F–1 were subsequently destroyed during nuclear tests, but the E–1 hole is still open to at least 609 m (Daniels et al., 1984).

After 1952 field study of the geology of the northern Marshall Islands was reduced significantly, although the nuclear testing continued through August 1958. The continued availability of Enewetak for future field studies was ensured by AEC's establishment in 1954 of the Enewetak Marine Biology Laboratory, now known as the Mid-Pacific Research Laboratory. The AEC completed some additional shallow drilling in 1953 and 1956 for soils engineering (Pratt and Cooper, 1968), but no more drilling for geologic study was completed until 1971. However, the vast amount of field data and samples yielded in the 1948 to 1952 efforts were studied and evaluated through 1964.

Formal presentation of the completed studies was compiled in the *USGS Professional Papers 260 Series* completed in 1964. This 28-paper series comprises the most comprehensive single body of geologic, geophysical, and oceanographic data ever assembled on a group of atolls. Much of the rest of this chapter will draw heavily on the data presented in these papers.

A major paper by Emery et al. (1954) is a comprehensive study of the surface geology of Bikini, Enewetak, and nearby atolls. It also presents data on the sediments of the lagoons, reefs and islands, reef morphologies and lithologies, and coral zonations of different reefs as well as many other topics. Also presented in the paper are the lithologic sections for the deep holes drilled on Bikini. Subsurface zones of calcitic limestones are described which are overlain and underlain by aragonitic sediments. These limestones are postulated to represent times of subaerial exposure of the atoll (Ladd et al., 1948; Emery et al., 1954).

Another paper in the 260 series by Munk and Sargent (1954) describes the variation in the spur and groove structure of the Bikini reefs and relates them to distribution and direction of wave energy. This relationship demonstrates that these are not relict Pleistocene erosional forms. Wells (1954) defined ecological zones of windward reefs in the northern Marshalls on the basis of dominant coral faunas and compared these zonations with reefs else-

where. The great organic productivity of atoll reefs versus the surrounding oceans is demonstrated by Sargent and Austin (1954).

The subsurface geology and geophysics of Enewetak Atoll somewhat dominates the 260 series. The penetration of a basaltic basement by drilling and the aeromagnetic and seismic refraction surveys indicated the presence of volcanoes beneath Enewetak, Bikini, and Kwajalein Atolls. Ladd and Schlanger (1960) present the locations and drilling data for the Enewetak drill holes. They conclude that most of the near surface material to 60 m depth is unconsolidated, whereas deeper zones of recrystallized and leached carbonate are postulated to represent periods of subaerial emergence of the atoll. Foraminifera were used to establish a Tertiary biostratigraphy of the Enewetak subsurface and to document continuous shallow water conditions in which the entire carbonate section had been deposited (Cole, 1957; Todd and Low, 1960). The oldest carbonates were identified as Upper Eocene in age.

The general subsurface geology of Enewetak was defined by Schlanger (1963), who presents detailed lithologic logs of the Enewetak deep holes and provides an interpretation of the geologic history. Schlanger (1963) noted the presence of numerous "solution unconformities" within the Enewetak geologic column. The term solution was used because Schlanger felt these unconformities represented karstic surfaces.

The scientific programs in the northern Marshalls had a stimulating effect on the academic interests in atolls. The interest in the geology and biology of carbonate reefs is still a dominant field of study. The geologic studies of this period answered many of the basic questions about atoll formation. Atolls rested on subsided volcanic foundations. The compositions and depositional environments of the subsurface sediments were characterized and interpreted. Specific zones of altered carbonates were identified and interpreted to represent periods of atoll emergence and given paleohydrologic meaning. Reef zonation and morphology, as products of interacting biological aggradation and mechanical and biological erosion, became better understood.

1964 to Present

Geological studies conducted during this time in the Marshall Islands have been centered on Enewetak Atoll. Numerous studies primarily concerned with sediment/organism interrelationships, the distribution of radionuclides within the atoll sediments, and geohydrology have been conducted under the auspices of the Mid-Pacific Research Laboratory, which is sponsored by the Department of Energy (DOE). The Defense Nuclear Agency has sponsored four major field programs to understand the craters resulting from the near-surface detonation of nuclear weapons: the Pacific Cratering Experiment (PACE), 1971 to 1972; the Exploratory Program on Enewetak (EXPOE), 1973 to 1974; the Enewetak Atoll Seismic Investigation (EASI), 1980; and the Pacific–Enewetak Atoll Craters Exploration (PEACE), 1984 to present.

Until the early 1970s, studies of Enewetak geology consisted of reviews or extensions of previous work. Gross and Tracey (1966) used stable carbon and oxygen isotope data to substantiate the hypothesis that the calcitic limestones in the subsurface were formed in fresh water environments (Ladd et al., 1948; Ladd and Schlanger, 1960; Schlanger, 1963). Thurber et al. (1965) performed U/Th radiometric dating of corals of the Enewetak subsurface from the Quaternary period and revealed an absence of corals dating between 6000 and 100,000 years before present (ybp), indicating a significant hiatus in deposition.

At Enewetak, PACE was conducted to evaluate the influence of the shallow subsurface geology on the dimensions of nuclear explosion craters. It consisted of two phases: (1) geological and geophysical investigations of the shallow (<70 m) subsurface of the atoll and (2) a series of high explosive cratering experiments. A federal court order cancelled PACE before most of the high explosive cratering experiments were conducted. However, much of the first phase was completed, and nearly 250 shallow boreholes were completed on seven islands, with 235 being drilled on Aomon or Runit Island (Henny et al., 1974). Most of the holes were soils engineering borings which returned little or no sample. Sample recovery in the cored boreholes was variable but was generally quite poor. A generalized four-layer engineering geology model for the shallow subsurface at Aomon Island was developed by Henny et al. (1974) using these limited samples and seismic refraction survey data.

The follow-on geologic and geophysical program to PACE was EXPOE. The objective of the EXPOE program was to develop a model of the near surface geology of the atoll for the nuclear crater regions in the northern islands. Forty-six cored boreholes and 13 water sampling wells were completed on 11 islands on the windward, leeward, and transitional sides of the atoll, and 250,000 lineal feet of shallow seismic refraction surveys were completed from 1973 to 1974. The EXPOE program was notable for the excellent sample recovery: recovery of 4-in. cores of both consolidated and unconsolidated materials averaged over 80% (Couch et al., 1975). This recovery was far greater than any previous drilling, especially in the poorly and unconsolidated near surface sediments, and allowed for a more detailed picture of the stratigraphy and petrology of the upper 100 m of the Enewetak subsurface than gained in previous studies (Ristvet et al., 1974, 1977).

As will be discussed in greater detail later in this chapter, the EXPOE findings indicate that the atoll periphery to at least 80 m depth consists of subordinate reef and dominant back reef and marginal lagoon deposits of the Holocene and Pleistocene ages. Five subaerial surfaces were recognized in the Pleistocene section associated with sea level drops during glacial periods (Ristvet et al., 1974, 1977).

The EASI field program consisted of overwater high resolution multichannel seismic reflection surveys of the KOA and OAK nuclear craters and the undisturbed lagoon off of Engebi (Enjebi) Island (Ristvet et al., 1980; Tremba

et al., 1982; Tremba, 1985) and participation in the MPRL sponsored R/V *Makali'i* submersible dives in 1981. The EASI seismic reflection profiles showed that shallow unconformities recognized in the EXPOE drilling continued across the lagoon paralleling the present day bathymetry. Additional deeper reflectors at 150 and 245 m and a series of reflectors between 320 and 365 m were noted and compared to the unconformities described by Schlanger (1963). It was hypothesized that the Middle Miocene reflectors between 320 and 365 m may be a representation of a series of closely spaced unconformities much like the Pleistocene section described for Enewetak and Bikini (Ristvet et al., 1974, 1977; Tracey and Ladd, 1974). Unfortunately, only deep drilling with high core/sample recovery would resolve this issue.

The PEACE program was a two-phase program with the objective of understanding the surface and subsurface morphologies of OAK and KOA nuclear craters. The first phase of the PEACE field program was performed during the summer of 1984 and included high resolution multichannel seismic reflection, bathymetric, side-scan sonar, and submersible studies primarily of the two cratered areas but included some studies of atoll-wide nature (Folger, 1986). The second phase of PEACE was conducted during the summer of 1985 and consisted of overwater drilling into and adjacent to the two nuclear craters. High core recovery was obtained in drill holes as deep as 490 m beneath the lagoon floor. The PEACE drilling data are in the analysis phase.

During this post-1964 period, Enewetak was the site of several geologic investigations sponsored by MPRL. Examples of these investigations include rates of calcification of the windward reef (Smith and Harrison, 1977), studies of Holocene sea level histories which suggest a higher than present sea level 4000 to 2200 ybp (Tracey and Ladd, 1974; Buddemeier et al., 1975), and investigations of the Quaternary history of the reef flat (Szabo et al., 1985). Submersible studies of the outer slope have been conducted by Colin et al. (1986) and Halley and Slater (1985) to define the morphology of the outer reef slope.

SURFACE GEOLOGY

General

Enewetak surficial geology is best divided on the basis of depositional environments: the outer slope, the reef, the islands, and the lagoon.

Outer Slope

The topography around Enewetak Atoll was first determined by 85 radial and five partially complete concentric lines of soundings made by the USS *Bowditch* in 1944 (Emery et al., 1954). The profiles show a steep slope of 18° to 49° from the reef edge to 450 m depth changing to a more gentle slope of 10° between 450 and 2000 m. Sediments collected from a profile seaward of the South Channel showed a predominance of fine grain and *Halimeda* debris to 1500 m depth (Emery et al., 1954).

In 1981, 22 submersible dives were made on the outer slope of the southern half of Enewetak to depths as great as 360 m (Colin et al., 1986). The outer slope was found to be quite steep, averaging about 60° between 90 and 360 m on the windward and transitional side and slightly greater on the leeward side. No terraces or grooves were noted below 30 m. Vertical grooves were noted on the leeward side below 150 m depth. Talus accumulations were noted below 150 m, with significant sediment slopes being found seaward of the South Channel below 200 m depth. Below 90 to 100 m depth, it appeared that no significant reef framework was being constructed. Significant quantities of sediment are being transported down the face of the outer slope on the windward side with little or none being transported on the leeward side.

In 1984 and 1985, Halley and Slater (1985) investigated the outer slope of the reef north of the MIKE nuclear crater utilizing the research submersible R/V *Delta*. Halley and Slater (1985) noted that the slope is characterized by three zones: (1) the reef plate, algal ridge and near fore reef, from sea level to 16 m depth with less than a 10° slope; (2) the by-pass slope, from 16 to 275 m, with slopes of 55° decreasing to 35° near the base; and (3) a debris slope less than 35° below 272 m depth.

Halley and Slater (1985) also examined an exposed cross section through the reef and fore reef deposits within a rockfall scarp created by the KOA nuclear detonation. The slump scarp exposes three stratigraphic units that are differentiated by the surficial appearance: (1) a near-vertical wall from the reef crest to 76 m that appears rubbly and is composed mainly of coral heads; (2) a vertical to overhanging wall from 76 to 220 m that is massive and fractured, producing smooth, blocky surfaces; and (3) inclined bedding below 220 m along which the slump block has fractured, exposing a dip slope of hard, dense white carbonate rock that extends to below 400 m. Caves occur in all three units. Fore reef boulder beds dipping seaward at 30° are truncated by the current outer slope surface, thus revealing the erosional nature of the by-pass slope.

Atoll Reefs

The Enewetak reefs, like those described elsewhere in the Marshalls and other localities in the world, show a strong zonation in bands parallel to the front (Emery et al., 1954). These bands are defined by both coral and coral–algal communities (Odum and Odum, 1955) and by sediment deposition patterns (Emery et al., 1954). Differences in the zonation types are recognizable for the three reef types: windward, leeward, and transitional. Most previous studies have concentrated on the zonation of the windward reef (Emery et al., 1954; Odum and Odum, 1955; Wells, 1954); however, description of the leeward and transitional reefs are presented by Emery et al. (1954).

Figure 2 presents the zonation of the windward reef. The zones consist of fore reef, algal ridge, coral–algal, reef

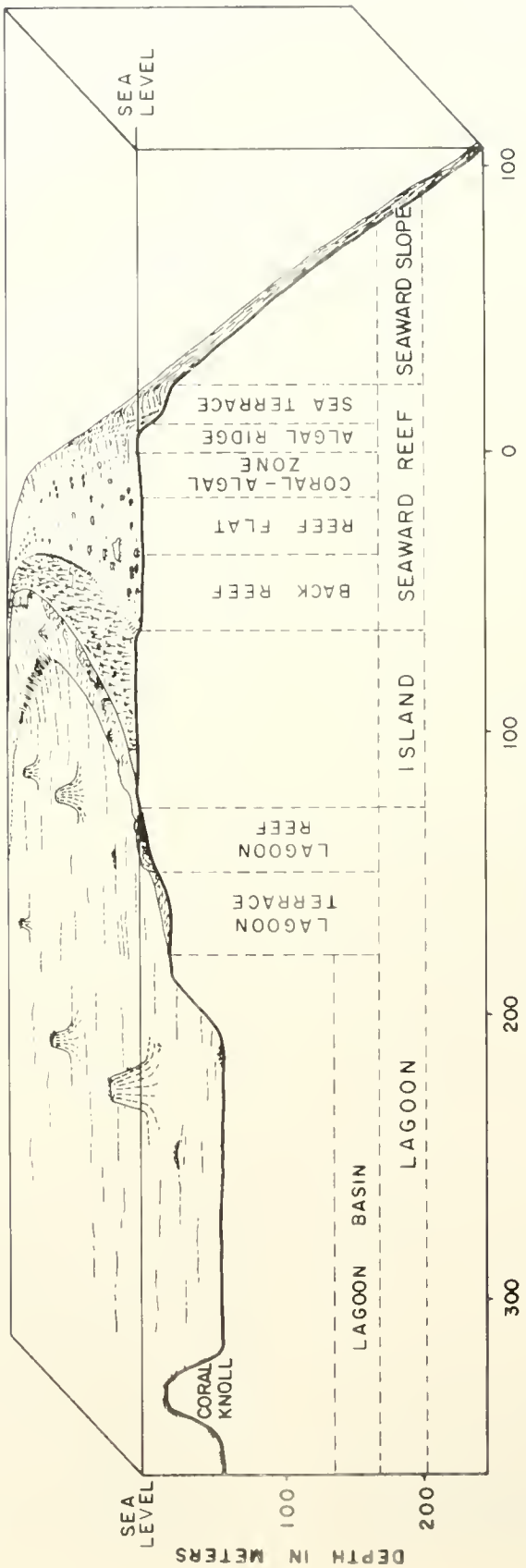

Fig. 2 Diagram of reef to lagoon zonation at Enewetak Atoll.

flat, and back reef flat. Figure 2 also displays the relationship of the reef to the islands and lagoon. Each of the five zones has unique biologic and geologic characteristics. Each of these zonations provides a model for what is seen in the subsurface. However, as will be seen in subsequent sections of this chapter, the Pleistocene subsurface appears to consist dominantly of subtidal deposits, whereas the modern reef flat consists of predominantly intertidal environments.

Tracey and Ladd (1974) and Buddemeier et al. (1975) present evidence that the broad intertidal, rocky platform of the modern windward reef flat consists of lithified subtidal sediments implying a previous higher-than-present Holocene sea level. The modern windward reef is an erosional platform developed after a growth of the Holocene reef to a higher sea level. Hence, there is the possibility that the modern Enewetak windward reef flat is not a good model to use to interpret former aggradational reef environments seen in the subsurface.

The windward fore reef consists of an area 30 to 50 m wide, sloping gently seaward at 10° to 15° and covered with coral and *Halimeda* sp. These gentle slopes do not exist on the leeward reef where the fore reef has 40° to 60° slopes. The same biological communities exist on the leeward fore reef as on the windward side (Colin et al., 1986). The fore reef extends to a depth of 30 m where the slope rapidly steepens, and the presence of stony corals and *Halimeda* declines drastically. At fairly regular intervals along the slope, there are nearly straight grooves perpendicular to the reef face. These grooves are from 2 to 3 m wide and 8 to 15 m long and are separated by spurs 5 to 10 m or more wide. The spurs are composed of living encrusting coralline algae (Emery et al., 1954). The origin of the grooves and spurs has been suggested by Munk and Sargent (1954) to dissipate the wave energy against the reef front. These grooves often extend into the algal ridge, especially on the transitional and leeward edges. The fore reef appears to be a site of active reef building with the sediments being cemented by biologic binding and penecontemporaneous marine cementation.

The algal ridge is primarily composed of encrusting red algae, primarily *Porolithon*. The algal ridge may actually grow above the reef flat elevation to as much as 0.3 to 0.6 m above the lowest low water due to wave action keeping the living algae wet during low water. The algal ridge with its biological and marine cementation provides the framework for the preservation of the back reef and lagoonal sediments from the erosion of ocean waves (Emery et al., 1954). Algal ridges occur on both the lagoon and ocean sides on the leeward reef. Both of these leeward algal ridges are poorly developed and do not rise much above the lowest low water.

On the inner side of the algal ridge, there is a belt of rich coral growth from 50 to 150 m wide. Stony corals cover more than 50% of the reef surface. Shallow pools contain most of the coral. The remainder of the zone is a pavement of encrusting red algae. The growth forms of the coral colonies are low or encrusting to withstand the wave action and low tides. Corals are predominantly *Acropora*, *Pocillopora*, and *Montipora*.

Again the coral–algal zone through biological and marine cementation provides well-cemented sediments for incorporation into the subsurface.

The windward reef flat at Enewetak is a fairly level rock surface that may be divided into two rather distinct parts: (1) a barren rock surface that appears to be the erosional surface of an older reef and (2) a rock substrate with a thin veneer of organisms, primarily the articulate red alga, *Jania*, giving the surface an appearance of being covered by a mat which Smith and Kinsey (1976) dubbed the "algal-turf."

Tracey and Ladd (1974) and Buddemeier et al. (1975) present evidence to support a higher-than-present sea level between 4000 to 2200 ybp. This higher sea level may have been 1 m or more greater than the present. The erosional nature of the present reef flat is postulated to be due to the lowering of sea level to near its present datum around 2000 ybp. Tracey and Ladd (1974) support their hypothesis with age dates of planed coral heads in the present windward reef flat seaward of Runit and Aomon Islands. Additional evidence is provided by Buddemeier et al. (1975), who through age dating show that much of the windward reef flat seaward of Aomon Island is composed of cemented subtidal deposits now present in an intertidal zone, the result of a recently lowered sea level. Additional evidence for a higher-than-present Holocene sea level around 4000 ybp for other Pacific islands may be found in Curray et al. (1970) and Chappell and Veeh (1978).

Despite its apparent erosional character, the present windward Enewetak reef flat is a highly productive reef environment in terms of the mass of carbonate sediments produced (Smith and Harrison, 1977). The algal–ridge, coral–algal zone, and the reef flat compose what is termed the "reef plate" (Henny et al., 1974). The reef plate consists of well-cemented rock resulting from penecontemporaneous biologic and marine cementation.

During PACE and EXPOE, several holes were drilled on the reef plate seaward of Aomon and Runit Islands. These holes, in addition to the outcrops exposed in quarries on the Enewetak, Medren, Runit, and Engebi (Enjebi) reef flats and the outcrops exposed in the LaCrosse nuclear crater on the Runit reef flat, show that the Holocene reef plate is a lagoonward prograding wedge of well-cemented sediments overlying unconsolidated subtidal carbonate sands and gravels. The seaward edge of the wedge begins approximately at the reef plate/coral–algal zone boundary. Within the shallow Quaternary subsurface, sediments beneath the coral–algal zone appear to be continuously well cemented with depth. Beneath the reef flat, the thickness of the wedge tapers from 3 to 4 m at the center of the reef flat to <1 m at the back reef/reef flat boundary (Ristvet et al., 1977).

The back reef is characterized by small to large solitary coral heads of *Porites* and *Heliopora* in a rocky to sandy substrate. Little or no marine cementation appears to be occurring, and the sands and silts have their origin from

sediment production and bioerosion of the reef flat. This environment extends from the reef flat to the islands.

Atoll Islands

The present islands of Enewetak represent wave and eolian deposits of excess sediment production from the reef stabilized in part by the formation of beachrock. Islands are present on the reef except on the northwest transitional reef. The islands are all approximately 3 to 4 m in elevation above the lowest low water. Two basic island shapes exist for Enewetak Atoll: (1) long linear islands that parallel the reef front, such as Runit, Enewetak, and Bokoluo and (2) the triangle-shaped islands with the base on the lagoon side parallel to the reef front and the point facing the seaward reef, such as Engebi (Enjebi), Aomon, and Louj. The origin of these two island shapes is not understood. The islands are covered with vegetation and have fairly well-developed soil profiles.

The origin of beachrock has been the subject of several investigations at Enewetak and other carbonate beaches in the world. Beachrock at Enewetak is present on 30 to 40% of all beaches. The formation of beachrock appears to be a fairly recent phenomenon with significant formation continuing today.

The author has collected samples of beachrock at Enewetak encapsulating World War II shell casings and cables from the nuclear testing period. The origin of beachrock was first investigated in the Marshalls by Emery et al. (1954), who looked at interstitial water chemistry and concluded that evaporation and heating of interstitial seawater resulted in carbonate precipitation. Schmalz (1971) studied the interstitial water of beach sediments on the lagoon side of Bijire Island in 1967. He concluded that precipitation of the dominant acicular aragonite and minor micritic magnesian calcite cements in the interstices of the carbonate sand was caused by the mixing of seawater with the brackish meteoric water in the thin Gyben–Herzberg lens. A succession of studies on the origin of beachrock cements followed Schmalz (1971). Commonly invoked processes for the precipitation of beachrock cements include evaporation of seawater, mixed fresh–saline waters, and vague types of biological involvement (Hanor, 1978). Current models show that degassing carbon dioxide from beach groundwaters appears to be the primary phenomenon that forms beachrock (Hanor, 1978).

Atoll Lagoon

The bathymetry of the lagoon was mapped in detail by the U. S. Navy in 1944. Nearly 180,000 soundings were made, and the results were contoured (Emery et al., 1954, chart 5). The lagoon bathymetry is somewhat irregular due to the presence of numerous coral knolls (patch and pinnacle reefs). The lagoon consists of four major bathymetric features: (1) lagoon terrace; (2) lagoon basin; (3) coral knolls; and (4) the reef openings.

The lagoon bathymetry shows a terrace between 15 and 22 m depth (Emery et al., 1954). The terrace borders all edges of the lagoon except the northwest and southern margins, where it is absent. The width is variable with 3 km being the greatest attained. The lagoon terrace is dotted with numerous patch reefs. The slopes from the islands to the terrace are gentle, averaging <2.5°. An even gentler slope, averaging 1.25°, separates the terrace from deep basin (Emery et al., 1954).

The main lagoon basin is a relatively flat area with slopes of 0.10°. The greatest depths are nearly 65 m in the northwestern half of the lagoon. The mean depth of the basin is approximately 55 m (Emery et al., 1954).

Within the lagoon are a large number of individual coral knolls or patch and pinnacle reefs. Emery et al. (1954) reported the presence of 2293 individual coral knolls. About 10% of the knolls rise to within 8 m of the surface. Most have tops between 30 and 36 m depth. The distribution of the coral knolls within the lagoon appears to be random. Seismic reflection profiles from EASI and PEACE through knolls suggest that they are predominately Holocene features. Nearly half of the knolls are formed over what is interpreted to be preexisting eroded Pleistocene patch or pinnacle reefs, whereas the other half of the lagoonal coral knolls do not appear to have an antecedent structure beneath them (Tremba, 1985; Grow et al., 1986).

The bottom sediments of the Enewetak Lagoon were first characterized by Emery et al. (1954) and most recently by T. W. Henry and B. R. Wardlaw (personal communication). Emery et al. (1954) found that the sediments consist of the following chief components: *Halimeda* sand, coral sand and gravel, foraminifera sand, mollusc shell sand and gravel, and fine debris. Fine debris was defined as all grains <0.25 mm in diameter. Emery et al. (1954) show the terrace to be dominated by fine debris and the basin by *Halimeda* and foraminifera sand. Henry and Wardlaw (1985) show a similar distribution but report much more mud-sized (<0.062 mm) carbonate sediment on the terraces and in the basin than Emery et al. (1954).

McMurtry et al. (1985) have investigated the magnitude of bioturbation of the lagoonal sediments off Runit Island and found that the burrowing shrimp of the family Callianassidae nearly completely mix and redistribute the surface sediments to a subbottom depth of at least 1.5 m.

SUBSURFACE GEOLOGY AND GEOPHYSICS

The subsurface geology of Enewetak Atoll consists of an approximately 1370 m thick carbonate sediment caprock overlying the summit of a basaltic volcano that rises 5000 m above the floor of the ocean (Ladd et al., 1953). Most of the drill hole data for the interpretation of the subsurface geology of Enewetak are derived from drilling on islands or the reef flat. The PEACE program has added data to 490 m subbottom depth on the northern lagoon terrace and northwestern shallow lagoon. The subsurface geology, as deduced from the analysis of the borehole samples and seismic profiles, is very similar to

the subsurface geology of Bikini Atoll (Emery et al., 1954) and Midway Atoll (Ladd et al., 1970).

Basement Rocks

In 1952, two deep holes (Fig. 3) reached the volcanic basement below the carbonate sediment caprock. Hole F–1 on Elugelab Island encountered hard basement rock at 1405 m depth. In hole E–1 on Medren Island, unweathered basalt cuttings were recovered from 1267 m, and solid basalt cores were taken from 1282.5 m to 1287 m. The basalt was an alkali olivine basalt containing analcime (Schlanger, 1963). The rock is similar to the late lavas of

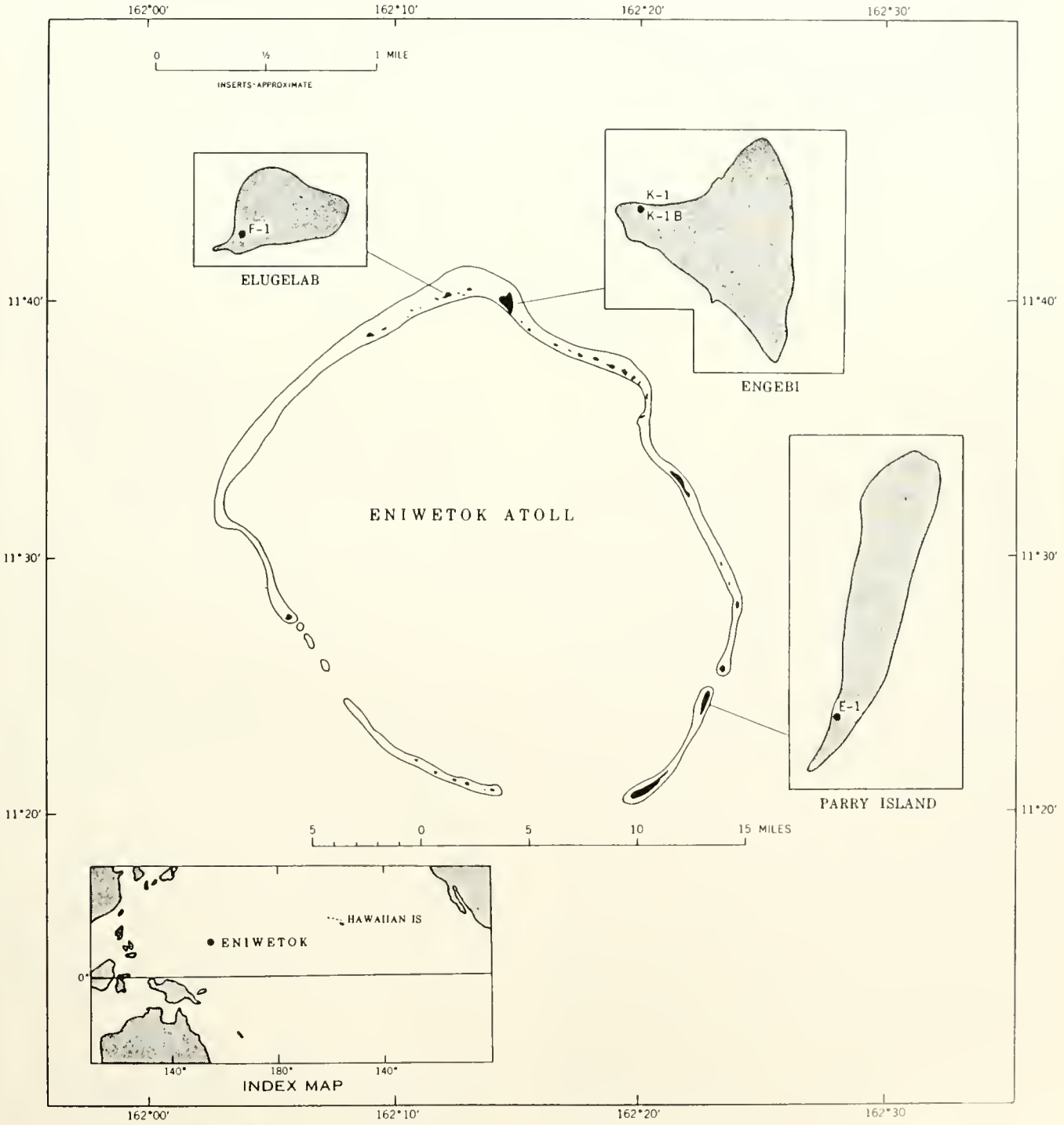

Fig. 3 Location map of three deep AEC holes drilled in 1951 and 1952. [From Ladd and Schlanger, 1960.]

the Hawaiian volcanoes and other islands of the central Pacific Ocean. Kulp (1963) found the basalt to be Eocene in age with a whole rock K/Ar radiometric date of 59 ± 2 million ybp and a pyroxene K/Ar date of 51 ± 5 million ybp.

The shape of the volcano is characterized by the two drill holes at the north and southeast edges of the atoll, the seismic refraction profiles of Raitt (1957) and the recent seismic reflection profiles of the PEACE program (Grow et al., 1986). Figure 4 displays the subsurface velocity structure of the atoll from the surface to the upper mantle as interpreted by Raitt. Although not depicted in Fig. 4, the uppermost velocity layer is a thin (105 m thick), low velocity (1920 m s^{-1}) unit detected beneath the reef northwest of Elugelab Island. The second and third layers have apparent harmonic mean velocities of 2440 m s^{-1} and 3050 m s^{-1}, respectively. Raitt (1957) suggests that both velocities are characteristic of partly consolidated calcareous sediments. The fourth through sixth layers comprise the volcanic basement underlying the carbonate caprock. Finally, the seventh layer has a seismic velocity, 8.1 km s^{-1}, characteristic of the upper mantle. Grow et al. (1986) show, in seismic reflection profiles, the top of the volcanics to be a relatively flat surface with only minor topograpy.

Carbonate Rocks

Figure 5 displays Schlanger's (1963) generalized interpretation of the subsurface of Enewetak Atoll based on the three deep holes drilled in 1951 and 1952. Also used for comparison is the interpretation of the subsurface of Bikini (Emery et al., 1954) which shows a strong similarity in the vertical extent of these zones for both atolls. Schlanger (1963) recognized that beneath both Enewetak and Bikini, there are zones characterized by the presence of fossil molds and solution features (leached and altered sediments) alternating vertically with zones containing primary skeletal aragonite (unaltered sediments) separated by relatively sharp boundaries. Schlanger (1963) termed the upper surfaces of the leached zones "solution unconformities," because they resemble karstic surfaces. Ladd et al. (1948) suggested that the leached zones at Bikini represented periods of atoll emergence and exposure of the marine sediments to subaerial conditions. The unaltered zones were believed to represent sediments that were never emergent.

Schlanger (1963) identified three major solution unconformities in the subsurface of Enewetak at depths of 850 m (Early Miocene), 335 m (Middle Miocene), and 90 m (Pleistocene) below the surface (Fig. 5). Schlanger (1963) also described an interval of partially leached and altered sediments within the upper 90 m of the Enewetak subsurface. However, due to limited sample recovery he was unable to identify a solution unconformity within this interval. He did conclude that at least one additional period of atoll emergence had occurred during the Pleistocene following the emergence related to the major solution unconformity at 90 m depth.

The high percentage of recognizable fossil material in the three deep drill holes allowed Schlanger (1963) to interpret the depositional environments of the sediments. Figure 6 presents the interpreted paleoecology of holes E–1 and F–1 at Enewetak and 2A–B at Bikini. The section of Eocene fore reef deposits in hole F–1 between 1280 and 1385 m represents outer slope deposits contemporaneous with near-reef, shallow-water deposits in hole E–1 from 845 to 950 m depth. The section of fore reef deposits in F–1 from 822 to 1280 m has no counterpart in E–1. Schlanger (1963) interpreted this as evidence that the earliest reef building at Enewetak began on the southeast side of the atoll near Enewetak and Medren Islands of today. Reef production and possible erosion of the southeast reef during the lower Miocene emergence resulted in the wedge of fore reef sediments seen in F–1. The seismic reflection studies of Grow et al. (1986) appear to confirm a prograding reef front from southeast to northwest starting in the presumed Eocene sediments and continuing to the Middle Miocene unconformity.

Post-Eocene carbonate sediments are all of shallow-water origin as sampled in the three deep holes, the EXPOE holes, and the PEACE holes. By the Middle Miocene unconformity, the location of the reef tract appears to have been very close to the present position of the modern day islands (B. R. Wardlaw, personal communication). In the substantial time represented by the upper 335 m of carbonate sediments, the reef tract has only migrated seaward 200 to 300 m. Deposition of shallow-water sediments under conditions of slow atoll subsidence continued through the Middle Miocene (Cole, 1957). However, the presence of several disconformities noted in the PEACE drilling from 335 to 490 m (T. W. Henry and B. R. Wardlaw, personal communication) and Schlanger's (1963) reported presence of recrystallized limestone from 603 to 650 m suggest some periods of atoll emergence.

Minor amounts of dolomitized limestone were noted within the Eocene stratigraphic section in both F–1 and E–1 and below the assumed Lower Miocene solution unconformity in F–1 (Schlanger, 1963). The dolomite appears as protodolomite replacing calcite. Schlanger (1963) felt that its origin may have resulted from the alteration of high magnesian coralline algae. Other hypotheses have been proposed including dolomite formation in the mixing zone of meteoric groundwaters with seawater during atoll emergence and/or formation from hypersaline conditions in a restricted shallow-water environment penecontemporaneous with deposition. Saller (1984) presents new evidence using stable Sr isotope data that the Enewetak dolomite precipitated from normal seawater significantly following deposition at burial depths greater than 900 m.

The 335 m unconformity described by Schlanger (1963) indicates a major emergence occurred after the deposition of Middle Miocene sediments. Ristvet et al. (1980) postulated, on the basis of the EASI seismic reflection profiles, that the 335 m solution unconformity con-

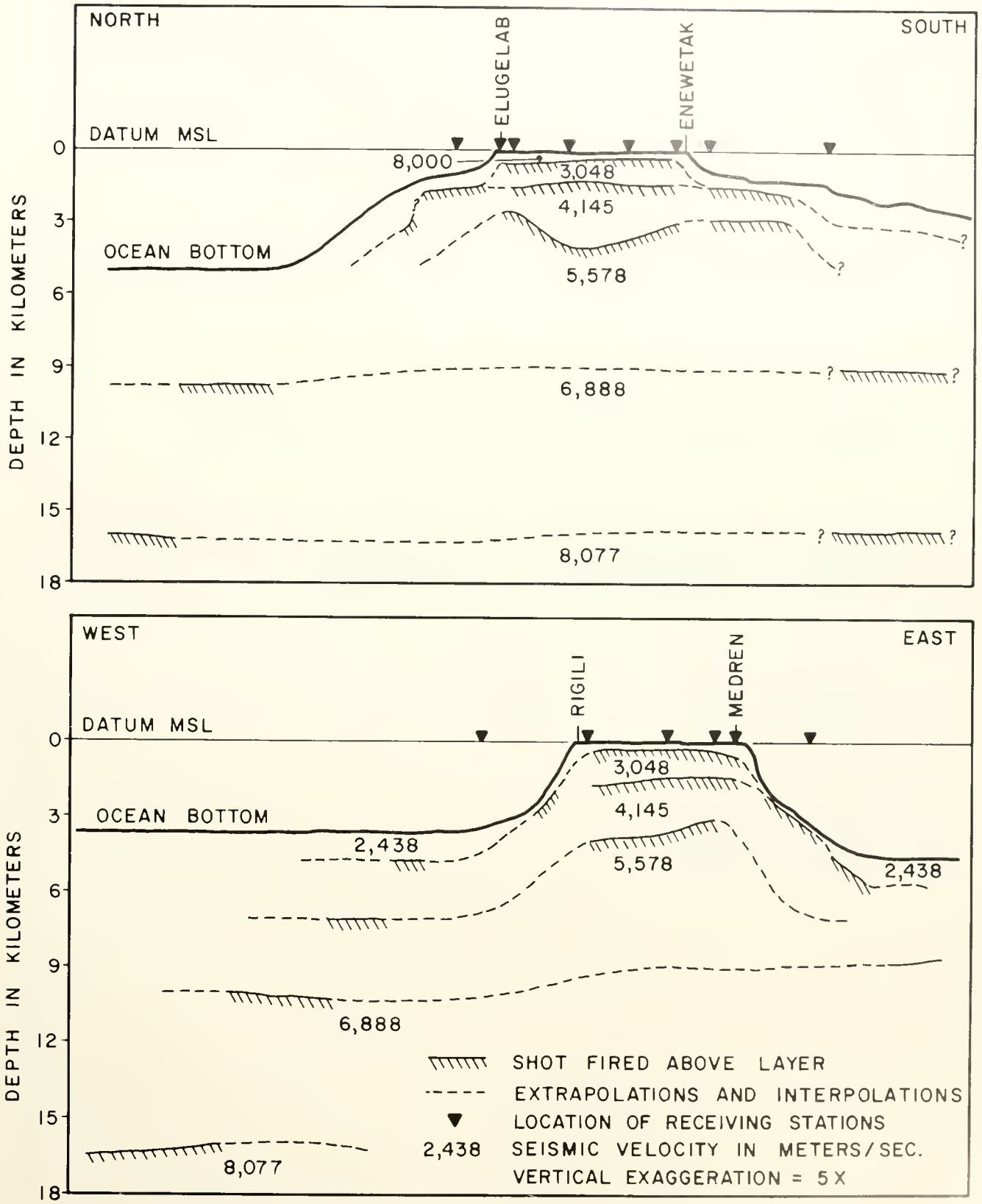

Fig. 4 Deep seismic refraction profiles of Enewetak Atoll. [Adapted from Raitt, 1957.]

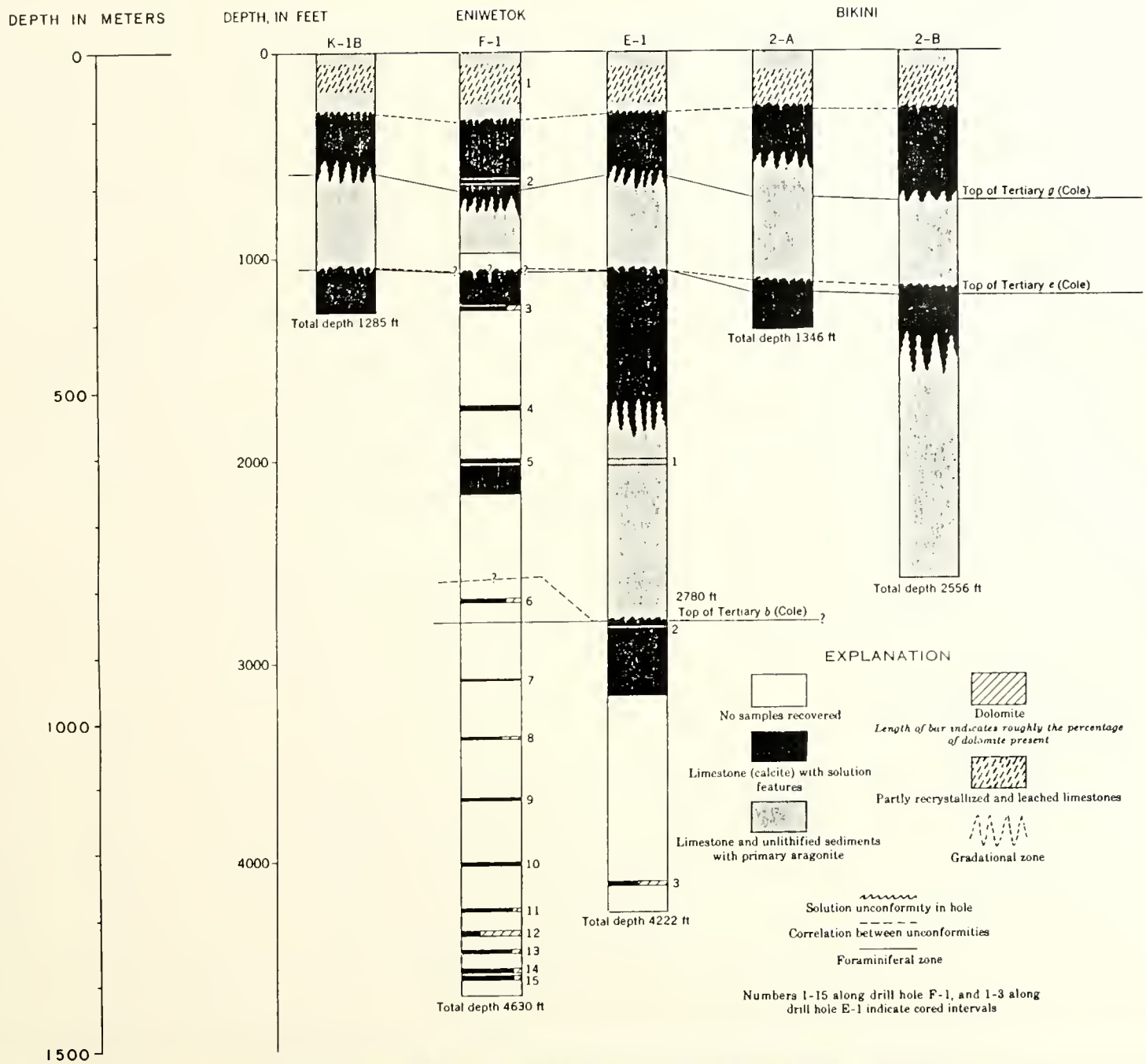

Fig. 5 Drill hole section of Enewetak and Bikini Atolls. [From Schlanger, 1963.]

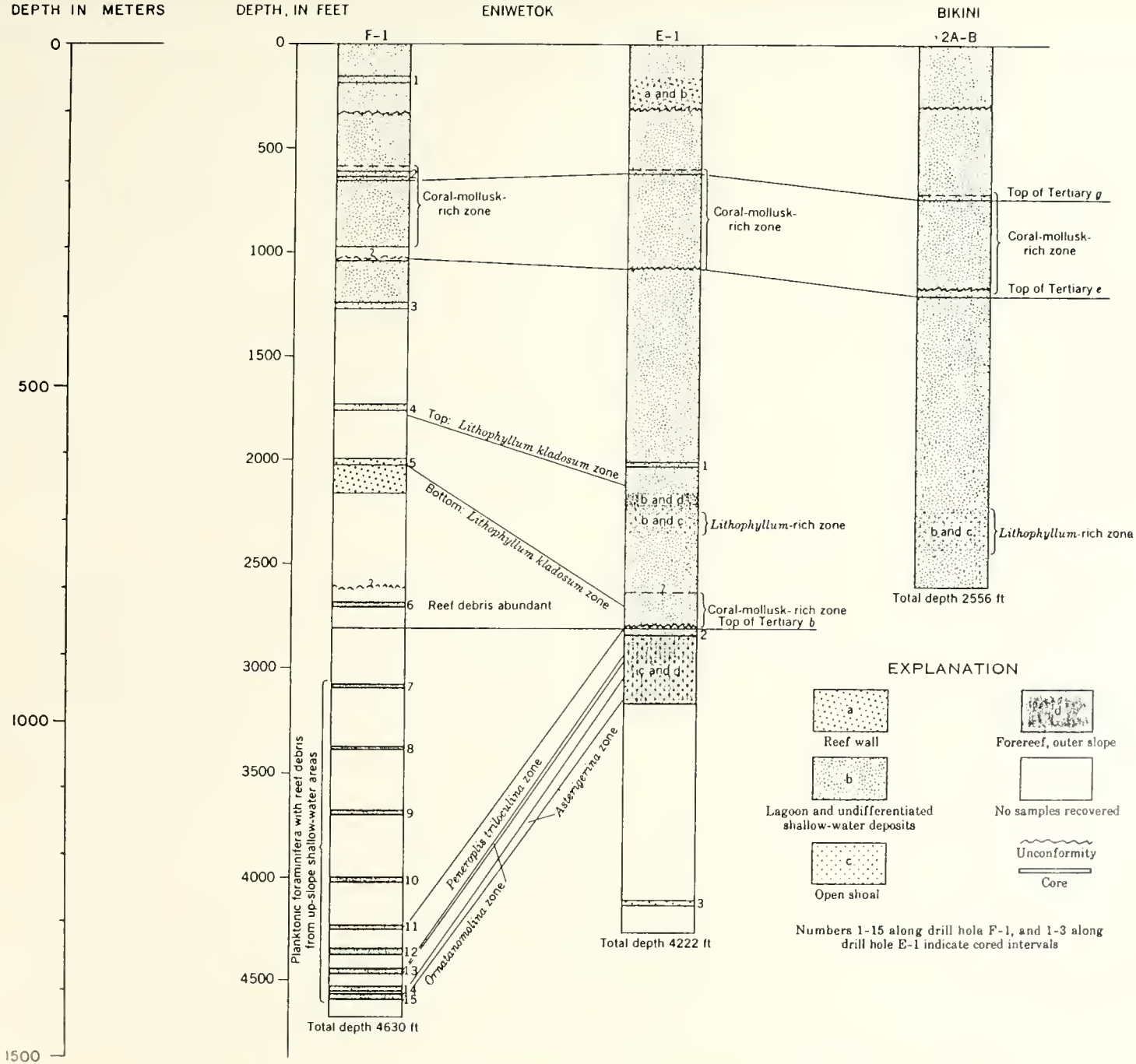

Fig. 6 Paleoecology interpretations of the drill holes at Enewetak and Bikini Atolls. [From Schlanger, 1963.]

sisted of several closely spaced unconformities similar to the Pleistocene section described by Ristvet et al. (1977). Preliminary results from the PEACE program show the presence of at least four subaerial surfaces between 310 and 350 m subbottom depths. This suggests that the Middle Miocene may have had episodic continental glaciation conditions similar to those well documented for the Pleistocene/Late Pliocene epochs. At least two of these unconformities show karstic features suggesting relatively long periods of subaerial exposure (B. R. Wardlaw, personal communication).

Resubmergence of the atoll occurred in Tertiary *f* time with the deposition of shallow-water sediments. From 210 to 252 m the sediments represent very organic-rich, normal lagoonal, or shallow-water deposits. Preliminary PEACE data suggest that the sea level did not fall during this depositional interval. Lignitic material is scattered throughout the interval. Leopold (1969) reported a polliniferous interval from the early deep holes from 205 to 270 m. This interval is interpreted as being a time when the atoll had rather large islands and large mangrove swamps developed (B. R. Wardlaw, personal communication). At a depth of more than 210 m, the sediments indicate normal shallow-water deposition and a return to the small island configuration.

Schlanger (1963) describes the presence of a major solution unconformity at a 90 m depth. Preliminary PEACE data show this to be the top of the Pliocene (T. M. Cronin, personal communication). A second subaerial exposure surface is recognized approximately 15 m below the 90 m solution unconformity.

The PEACE drilling program has provided nearly continuous sampling of the upper 490 m of the Enewetak subsurface near its northern and northwestern lagoonal edges. Unfortunately, results of this recent drilling program are still forthcoming. Preliminary results of the PEACE drilling confirm the general interpretations made by Schlanger (1963); however, they provide a significant increase in the detailed understanding of the post-Lower Miocene stratigraphic section unavailable to Schlanger (1963) due to the poor sample recovery of the 1951 and 1952 drilling. It is anticipated that the PEACE results will lead to redefinition of the biostratigraphy, based both on foraminifera and ostracods of the post-Eocene of Enewetak and the Pacific in general. A detailed understanding of the Enewetak sea level history will also be forthcoming as well as additional insight into the processes of the diagenesis of carbonate sediments.

The Quaternary subsurface of Enewetak is well-defined by the data obtained during the EXPOE drilling and is now further supplemented by the PEACE drilling. Five major unconformities were recognized by Ristvet et al. (1974, 1977); Goter (1979); and Szabo et al. (1985). Figure 7 presents an ocean reef to lagoon cross section across Engebi (Enjebi) Island constructed from the logs of EXPOE drill holes (Couch et al., 1975) and supplemented by data from the geologic redescriptions of several of these holes for the PEACE program (B. R. Wardlaw, personal communication). Each of the five unconformities represents paleosubaerial exposure surface and is marked by the presence of paleosols (terra rosa type), soil base features (laminated crusts, rhizoconcretions, etc.), and/or prominent changes in the mineralogical and chemical composition and cementation of the sediments. These five unconformities are within the upper zone of leached and altered sediments described by Schlanger (1963). Because of the excellent core recovery during the EXPOE drilling, the identification of these Quaternary unconformities was easily made. Szabo et al. (1985) have dated three of the first four lithosomes using a variety of radiochemical techniques. These ages are shown in Fig. 7.

The first unconformity at approximately 10 m depth is the Holocene/Pleistocene contact. Radiocarbon dates indicate that the Holocene sea transgressed the emergent platform reef by about 8000 ybp. The reef grew rapidly upward (about 5 to 10 mm yr^{-1}) until approximately 6500 ybp. Following 6500 ybp, vertical growth slowed to about 0.5 mm yr^{-1} prompting lateral development of the reef (Szabo et al., 1985; Tracey and Ladd, 1974). As previously discussed, sea level may have been nearly 1 m higher than present between 4000 and 2200 ybp. Current relative sea level rise at Enewetak may be near that of the long-term subsidence rate of 0.02 to 0.04 mm yr^{-1} (Buddemeier et al., 1975). Smith and Kinsey (1976) estimate that the present Enewetak reef has potential for upward growth of approximately 1 mm yr^{-1}. The difference in growth potential versus modern relative sea level rise may explain why the reef plate is prograding lagoonward as noted by Ristvet et al. (1977) for the windward reef off Runit and Aomon.

Pleistocene rocks in the lithosome directly below the first unconformity are dated at 131,000 ± 3000 ybp by Szabo et al. (1985) and 100,000 to 120,000 ybp by Thurber et al. (1965). There is also a significant change in the mineralogical and chemical composition of the sediments below this first unconformity versus the Holocene sediments above. Ristvet et al. (1974) document the near total loss of high-magnesian calcite below this layer and significant decreases in the whole rock trace element concentrations of Mg, Fe, and Mn. Calcitic vadose and phreatic carbonate cements are first encountered in this lithosome.

The development of the unconformities and the associated diagenesis of the underlying carbonate sediments are the result of relative sea level changes during the past. Periods of worldwide continental glaciations cause a lowering of sea level. At Enewetak during the Quaternary, this may have been in excess of 100 m (Walcott, 1972) during each major glacial advance. During these periods of sea level lowstands, the Enewetak Lagoon is above sea level and the atoll becomes a large, high carbonate island, resulting in severe changes to both the hydrologic regime and sediment production of the atoll. Because the reefs are subaerially exposed, only minor reef growth occurs as a fringing reef on the outer slopes of the atoll–island. The atoll–island undergoes subaerial erosion and soil develop-

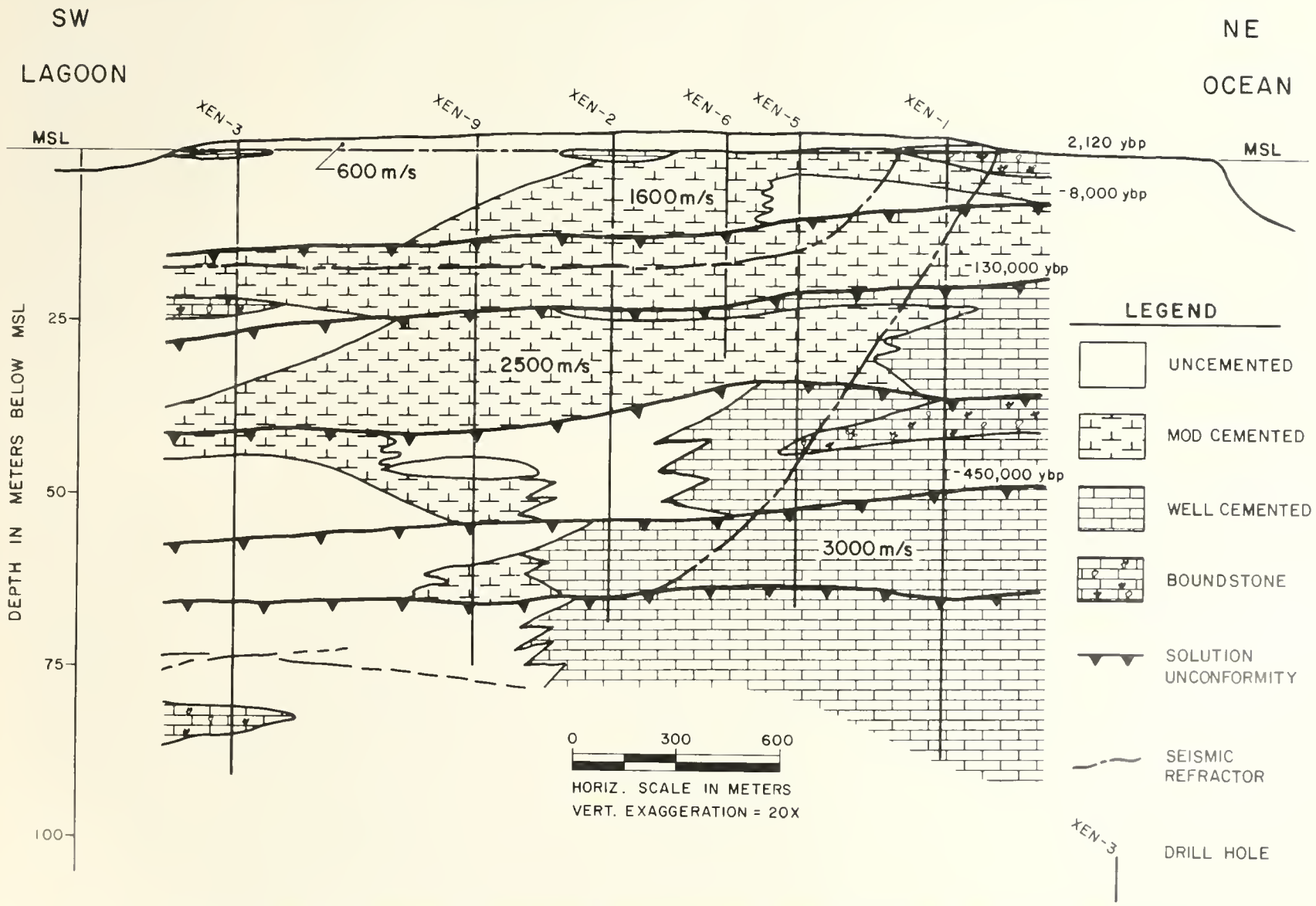

Fig. 7 Geologic cross section of the Quaternary of Engebi (Enjebi) Island with seismic velocities and ages dates indicated. [From Ristvet et al., 1977.]

ment from eolian sources. Such subaerial exposure to meteoric waters results in the development of an extensive Gyben–Herzberg lens within the island which is conducive to the alteration and cementation of the sediments.

During atoll emergence, several processes acting alone or in various combinations can produce significant modifications in those carbonate sediments exposed to meteoric waters. Most of these processes are dependent on the initial dissolution of carbonate minerals into an aqueous phase. Subsequent precipitation of calcium carbonate may be caused by changes in carbon dioxide pressure, temperature, evaporation, mixing of waters of differing ionic strength, and other mechanisms (Bathhurst, 1971). Precipitation appears to be highly variable in both space and time. It may be contemporaneous with dissolution or may involve transport over large distances.

The model proposed for the diagenesis of Enewetak sediments is similar to that proposed for other carbonate sequences (Thorstenson et al., 1972). Meteoric waters passing through a soil approach equilibrium with the ambient CO_2 pressure which is normally significantly higher than atmospheric CO_2. These high CO_2 waters promote dissolution of the metastable aragonite and magnesian calcite mineralogy of recent carbonate sediments and approach equilibrium solubility. The saturated waters at a later stage encounter an environment of lower CO_2, causing degassing of CO_2 and the subsequent precipitation of calcite. The process of CO_2 control on solution–precipitation of carbonates occurs within both the vadose and phraetic zones. At standard pressures and temperatures, the loss of high-magnesian calcite to calcite generally precedes the solution of aragonite and the concurrent development of moldic porosity before the precipitation of calcite.

As may be seen in Fig. 7, several periods of atoll emergence have been followed by submergence during the Quaternary. For the Quaternary, it appears that following each sea level rise, the new depositional environment parallels that below the unconformity and buries it with new sediments as the platform subsides. The processes involved in subaerial diagenesis of the sediments during each period of emergence are multiple upon the older lithosome below each unconformity. In other words, for any depth within the meteoric vadose and phraetic regime, there is a potential for the solution reprecipitation process to occur as many times as there are subaerial exposures above that depth. This multiple diagenesis results in progressive increases in cementation and mineral stability with increasing depth for at least the Quaternary section of the Enewetak subsurface.

The Quaternary subsurface of Engebi (Enjebi) (Fig. 7) consists of a complex mosaic of depositional lithofacies, which have subsequently been affected by diagenetic processes. In general, cementation increases with depth and towards the reef within each stratigraphic unit. This lateral change in cementation and, as shown by Ristvet et al. (1974), corresponding changes in the rates of mineral stabilization and trace element petrochemistry may be in part due to (1) the occurrence of marine cements in those sediments near the reef flat versus those deposited lagoonward and (2) to diagenetic processes affecting the sediments as a function of the paleohydrologic regime and the paleochemistry of the meteoric lens (Ristvet et al., 1977).

Shallow seismic refraction surveys were conducted on windward, leeward, and transitional islands during EXPOE and yielded consistent profiles for the Quaternary Enewetak subsurface (Ristvet et al., 1977). As shown on Fig. 7, four distinct velocity intervals exist. The velocity in the unsaturated island sediments, V_0, is 330 to 600 m s^{-1}; V_1 is the velocity in saturated, unconsolidated Holocene sediments and is typically about 1600 m s^{-1}. The velocity in poorly to moderately cemented Pleistocene sediments, V_2, is typically 2500 m s^{-1}. The V_1/V_2 interface corresponds to the first unconformity. The higher velocities of well-cemented sediments which occur on the reefward side of the island and at depths below 60 m as inferred from lithologic descriptions of drill holes are represented by V_3 (Ristvet et al., 1977).

The unconformities recognized by the drilling on the atoll edges may also be followed into the lagoon on seismic reflection profiles obtained during EASI and PEACE (Ristvet et al., 1980; Tremba et al., 1982; Tremba, 1985; Grow et al., 1986). Figure 8 is the interpretation of a seismic reflection record which is a lagoonward extension of the Engebi (Enjebi) reef to lagoon geologic cross section shown in Fig. 7. The seismic profile is perpendicular to the reef front and crosses the lagoonal terrace into the lagoon basin. In Fig. 8, the first reflector/refractor corresponds to the Holocene/Pleistocene unconformity at 15 m subbottom depth. The reflector at 66 m subbottom depth seems to correspond to a Pleistocene unconformity seen in the Engebi (Enjebi) drill holes. From the PEACE drilling, it is apparent that the deeper reflectors between 150 and 330 m correspond to lithologic changes and do not necessarily represent unconformities. The 330 m reflector does represent the top of a series of closely spaced reflectors corresponding to the Middle Miocene unconformities recognized in the PEACE boreholes. Of interest is that parallelism of the reflectors to the present bathymetry. This feature of the seismic records was noted atoll-wide for reflectors above the Middle Miocene unconformities helping to confirm the hypothesis that the present-day reef environments have shown little lateral migration since the Middle Miocene.

GEOHYDROLOGY

Studies of the hydrology of Enewetak Atoll were initiated in 1972 to evaluate possible environmental effects of the proposed PACE high explosive craters on the groundwater resources of the islands (Koopman, 1973). Additional studies sponsored by the DOE have been conducted as part of a program to determine the physical, chemical, and biological mechanisms controlling the distribution and transport of radionuclides in the atoll environment (cf. Buddemeier and Holladay, 1977; Wheatcraft and Buddemeier,

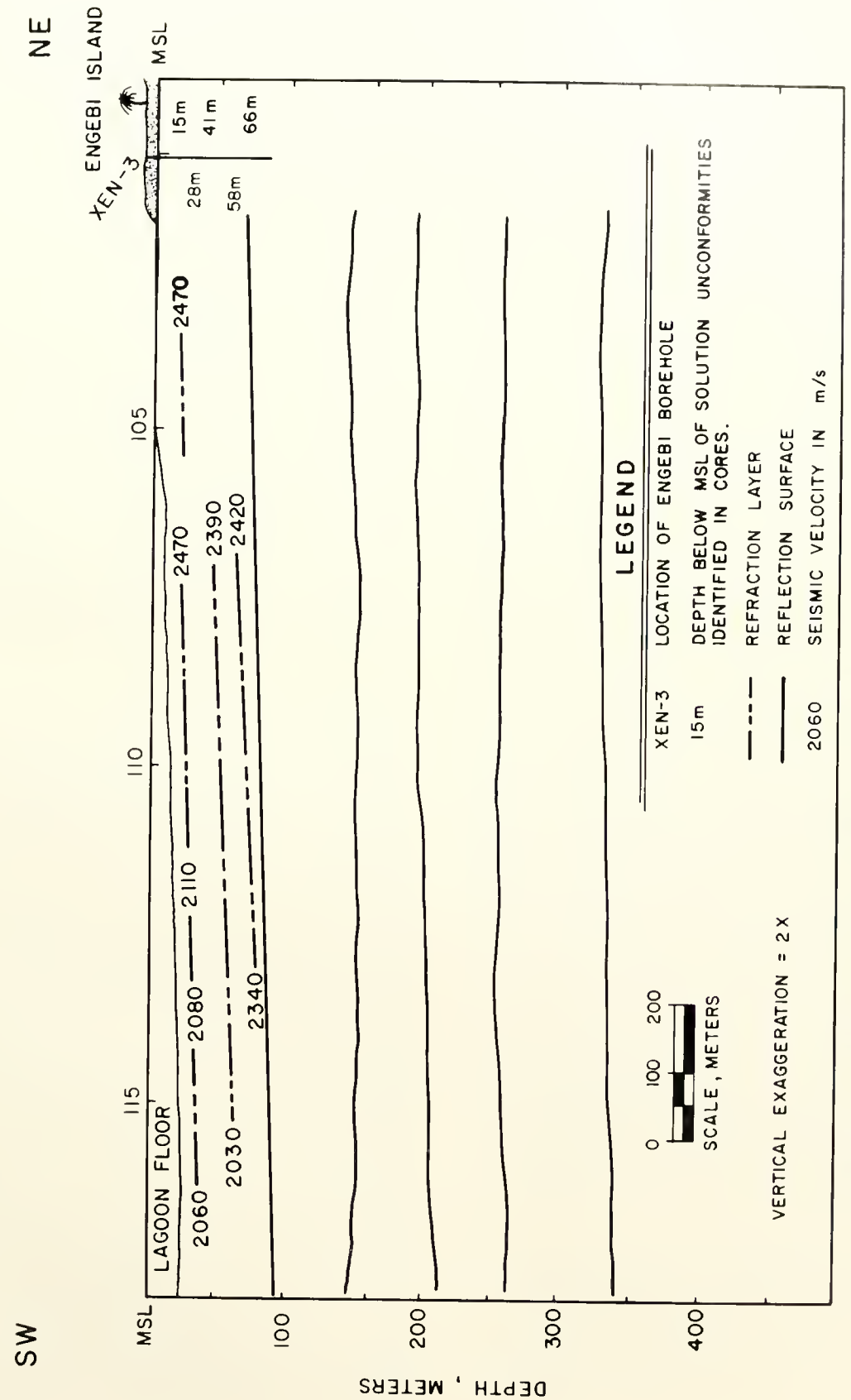

Fig. 8 Interpreted seismic reflection/refraction profiles in lagoon off Engebi (Enjebi). [From Tremba et al., 1982.]

1981; Buddemeier, 1981). An additional study was sponsored by the DNA (Buddemeier and Jansen, 1976) to investigate the groundwater potential for use in the Enewetak Radiological Cleanup.

Atkinson et al. (1981) investigated the water budget and circulation of water in the Enewetak Lagoon and found that essentially all the water input to the lagoonal system comes from wind-driven transport across the windward reef. Since the windward reef crest is typically near mean sea level, waves drive water from the ocean into the lagoon at nearly all times. The windward reef blocks any return flow. Atkinson et al. (1981) determined that nearly all of the outflow occurs through the South Channel. The Deep Channel had a balanced inflow and outflow. Other input/output pathways, i.e., transport over the leeward reef was insignificant in comparison to input over the windward reef and output through the South Channel. Atkinson et al. (1981) calculated a mean residence time for lagoon waters of 1 month with a maximum of 4 months for water in the northeast section of the lagoon. Although water levels were not directly observed, the circulation pattern requires the existence of a net lagoon to ocean gradient (Buddemeier, 1981).

Koopman (1973) first noted that, for the islands of Enewetak, a significant discrepancy existed between the calculated thicknesses of a fresh water Gyben–Herzberg lens and that observed in trenches and borings in the field. Koopman (1973) observed that the islands of Engebi (Enjebi) and Aomon had only thin brackish water lenses approximately one-tenth as thick as would be predicted using conservative calculations. Buddemeier and Holladay (1977) measured tidal lags in wells on Engebi (Enjebi) Island and noted that there was a sharp discontinuity in the plot of tidal lag time versus depth between 10 and 20 m subsurface depth. They hypothesized that the effect might be due to a more permeable aquifer below the first unconformity of Ristvet et al. (1977). Wheatcraft and Buddemeier (1981) demonstrated, using tidal data from Engebi (Enjebi) Island, that the classical Gyben–Herzberg lens model does not describe the hydrologic system observed, which is controlled by vertical transmission of tidal signals from deeper and more permeable Pleistocene aquifer(s).

Buddemeier (1981) noted that total fresh water content of island groundwater was essentially independent of island area and radius and that the southern islands have approximately 50% more fresh water volume than the northern islands. In addition to this difference in gross fresh water inventory, Buddemeier (1981) noted the northern islands have thinner layers of potable water and more extensive brackish water transition zones than do the southern islands.

Buddemeier (1981) made additional tidal measurements on Japtan, Biken (Rigili), Enewetak, Aomon, and Engebi (Enjebi) Islands and concluded that significant differences were present between the amplitudes of reef and lagoon tide stations on the falling tide resulting in a net lagoon to ocean head. Buddemeier (1981) concluded that this net head of water will tend to set up a lagoon to ocean flow of water through the permeable Pleistocene aquifer and that the amount and quality of fresh island groundwater is controlled by the rate of lagoon to ocean flow through the Pleistocene aquifer. The estimated lagoon to ocean transit times are on the order of 3 to 6 years, which corresponds well to the fresh water residence time estimates of the islands based on inventory and recharge. The rate of flow from lagoon to ocean dependency explains why islands in close proximity to reef channels, such as the southern islands, have greater volumes of fresh water than others.

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Chapter 5

Oceanography of Enewetak Atoll

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INTRODUCTION

Enewetak and Bikini lagoons are large, deep atoll lagoons. The circulation systems of both lagoons are dominated by wind-driven currents (von Arx, 1948, for Bikini, Atkinson et al., 1981, for Enewetak). However, the full dynamics of the Enewetak circulation system is explained by a combination of wind-driven currents, slope currents from water input by waves, and tidal currents. The findings at Enewetak indicate that the internal circulation and flushing of deep atoll lagoons is affected by atoll morphology and local wave and tidal conditions, features which in general control circulation in shallow atoll lagoons (Milliman, 1967; Gallagher et al., 1971; Henderson et al., 1978; Ludington, 1979).

This chapter begins with the general oceanography of the northern Marshall Islands and then concentrates on the oceanography of Enewetak Lagoon. The oceanography of Bikini Lagoon and vicinity have been well studied compared to Enewetak. In this chapter frequent comparisons are made between Enewetak and Bikini.

NORTH EQUATORIAL CURRENT

Enewetak resides in the North Equatorial Current. In the region of the Marshall Islands, the current is between 6° to 8° and 15° to 17° north latitude. The southern boundary of the current moves northward with the sun during northern hemisphere summer and shifts back toward the south in winter. The current has a general westward drift between 20 to 50 cm s^{-1}. Surface water is isothermal to 75 m and varies seasonally between 26° and 29°C. The main thermocline is between 150 and 300 m with a temperature of 10°C at 300 m. By 1500 m the temperature drops to 3°C.

Between the region of 3° to 11°N the salinity is relatively low (34.1 to 34.5 $^{0}/_{00}$) reflecting the annual net rainfall in the region and the eastern flow of the Equatorial Countercurrent. Higher salinities occur to the north of 11° (the latitude of Enewetak) due to increased evaporation. Isohalines show development of Intermediate Water about 11°N. Figure 1 shows the temperature–salinity relationships of the Western North Pacific Central Water and Pacific Equatorial Water in the region of the northern Marshall Islands (Barnes et al., 1948). The solid lines in the diagram indicate the temperature–salinity correlations at different latitudes; at 20°N the water is all North Pacific Water and at 4°N it is all Pacific Equatorial Water. The insert in the diagram shows the depth of transition zones between the two water masses. Enewetak Atoll resides in the region where the transition zone is above 200 m and is only 50 m thick (Barnes et al., 1948).

Dynamic topography near Enewetak has never been measured. However, data collected during the Operation Crossroads project and by the Japanese indicate dynamic topography to be complex near Bikini, with the presence of eddies northwest and northeast of the atoll (Barnes et al., 1948). Rather permanent eddies probably exist near Enewetak because they do for other islands (Hamner and Hauri, 1981). The complexity of dynamic heights suggests that currents near the atolls may vary in both speed and direction.

WAVES AND TIDES

Waves formed by the northeast trade winds break on the northern and eastern reef perimeters of the atoll. This constant pounding of the fore-reef shapes the spurs and grooves on the windward side. For Bikini Atoll, Munk and Sargent (1949) used wind data to calculate wave direction, wave height, and wave energy. The spur and groove systems on the windward side of Bikini dissipate 95% of the calculated wave energy as frictional heat and channel 5% of the energy upward to maintain a head of water on the reef flat. The head of water establishes water flow from the ocean to lagoon across the windward reef flats. Waves within the lagoon are generated by local wind patterns and have little influence in shaping the reef structures, but they do influence sand transport.

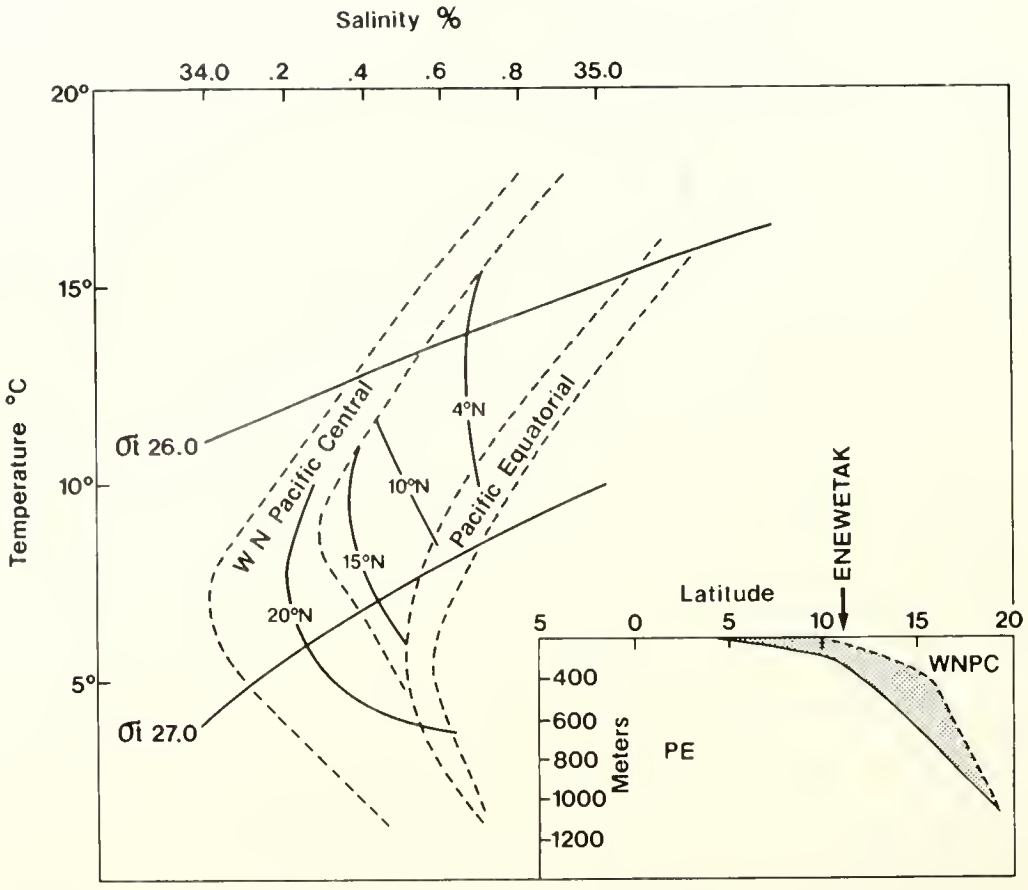

Fig. 1 Temperature-salinity relationships of Western North Pacific Central Water (WNPC) and Pacific Equatorial Water (PE) in the region of the northern Marshall Islands. The solid lines show the temperature-salinity relationship at different latitudes. The insert shows depth of transition zone between the water masses. [Drawn from Barnes et al., 1949.]

Breaking waves on the fore-reef and the back-reef determine sand transport in the following ways. Cross-reef currents carry sand from the fore-reef and the reef flat to the lagoonward rim of the reef, building and eroding islands. Ephemeral sand spits develop on the margins of the islands; this sand is sorted and distributed by long-shore transport from lagoon waves and back-reef currents. Two general patterns of sand grain size have been determined for Bikini (Emery et al., 1954): (1) grain size increases across the reef flat from ocean to lagoon, then inside the lagoon, grain size decreases until a depth of approximately 15 m is reached; and (2) grain size decreases from the middle of the seaward beaches toward the ends of the islands and decreases from each end of the island to the middle of the lagoon beach.

Two processes are apparently responsible for the distribution of sand: (1) high energy cross-reef currents carry a large suspended load, depositing sand as they slow down; and (2) the continual breaking of seaward and lagoonward waves on the islands transports sand along the shore. The high energy currents are formed from oceanic swells breaking on the fore-reef, and the long-shore currents are formed by lagoon wind waves breaking on the beach. In the future, sand transport by currents at Enewetak could be studied as a function of wind speed and direction, surf height, and swell direction.

The tides at Enewetak Island are usually in good agreement with the U. S. Navy Tide Tables. However, lagoon and ocean tide records show differences in amplitude, timing, and tide curve shape. When the reef is awash at Enjebi, wave set-up produces ocean tides with a mean water level 0.3 to 0.5 m above the mean lagoon level; at Enewetak Island, the differences are small but significant (Buddemeier, 1981) (Fig. 2). Buddemeier also analyzed long-term differences between the Japtan gauge and a lagoon gauge at Biken (see Fig. 2 for location). His analysis showed that while the tide records were similar in amplitude and frequency composition, the Biken highs are broadened and the lows narrowed by about 1 hour. Based on an average difference in tide elevation between Japtan

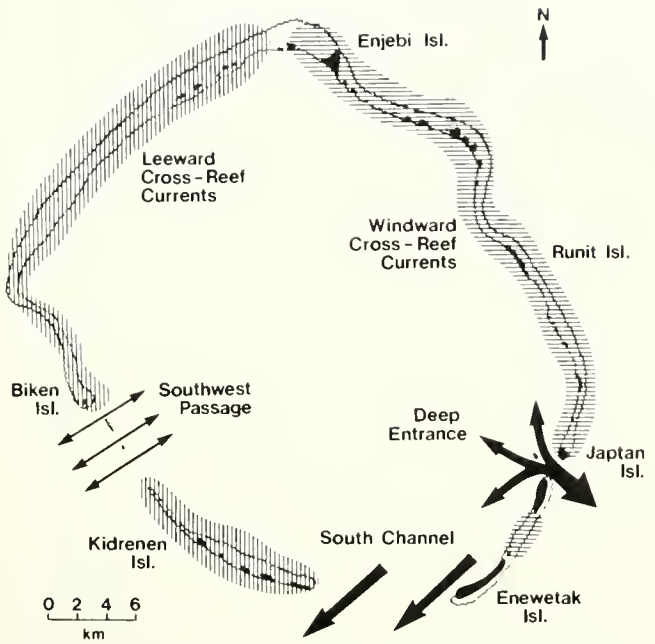

Fig. 2 Location of islands and currents. See text for discussion. [From Atkinson et al. with permission.]

and Biken, Buddemeier estimated that the water level is about 6.5 cm higher at Biken than at Japtan.

LAGOON WATER

The lagoon at Enewetak is well isolated from the general westward flow of the North Equatorial Current. The reef flats are shallow (0 to 2 m deep), and the deepest part of the Deep Entrance is about 57 m. Because the surface North Equatorial Water is well mixed to a depth of 75 m, water flowing into the lagoon, either over the reefs or through the channels, is well-mixed ocean surface water. Salinity, temperature, dissolved inorganic plant nutrients, and dissolved carbon dioxide suggest little stratification within the lagoon water (Table 1). For the data at hand, surface water (0 to 10 m) appears to be slightly cooler (0.2°C) and less saline (0.06 $^{0}/_{00}$) than deeper water. During the data collection period (July 26 to August 16, 1974), the weather was unusually rainy and cool (S. V. Smith, personal communication). August is a period of low wind; therefore, stratification should occur most dramatically during this month, yet no major stratification is evident in these data. There is only a slight indication of the rain in the surface water. Nutrient data collected by S. V. Smith and M. J. Atkinson during June 1979 in the lagoon and passages also showed no vertical structure. Several detailed nutrient profiles taken between 0 to 2 m above the bottom, at 10 cm intervals, revealed extremely low and unchanging concentrations. Vertically averaged phosphate and nitrate–nitrite concentrations are contoured and suggest a weak minimum toward the center of the lagoon (Fig. 3).

CURRENTS

Cross-Reef Currents

Cross-reef currents involve shallow flow over the windward and leeward reef margins of the atoll. The area of

TABLE 1

Chemical Data for Ocean and Lagoon Water*

	Temp (°C)	Sal ($^{0}/_{00}$)	Total alk (eq m^{-3})	PO_4	NO_3	NH_4	Si	pH	Total CO_2 (moles m^{-3})	P_{CO_2} (uatm)
				(mmoles m^{-3})						
Ocean										
Surface	29.5	34.30	2.29	0.12	0.21	0.50	4.4	8.31	1.88	297
S. Dev.	0.2	0.04	0.03	0.05	0.12	0.20	2.3	0.02	0.04	22
N.	7	7	7	6	6	5	7	7	7	7
Lagoon										
Surface (0.10 m)	29.6	34.22	2.29	0.14	0.15	0.37	3.4	8.29	1.89	313
S. Dev.	0.5	0.19	0.05	0.05	0.08	0.21	1.9	0.04	0.04	31
N.	125	117	118	116	111	101	118	118	116	116
Mid-depth (10 to 30 m)	29.8	34.28	2.31	0.13	0.13	0.28	3.4	8.25	1.90	311
S. Dev.	0.5	0.08	0.05	0.04	0.07	0.17	1.7	0.04	0.03	38
N.	56	56	56	56	55	53	56	56	56	56
Deep (30 to 50 m)	29.7	34.28	2.30	0.15	0.18	0.27	3.4	8.27	1.91	336
S. Dev.	0.3	0.08	0.04	0.05	0.12	0.19	1.8	0.03	0.03	26
N.	28	27	28	27	27	26	28	28	28	28

*Data collected by S. V. Smith, July and August 1974.

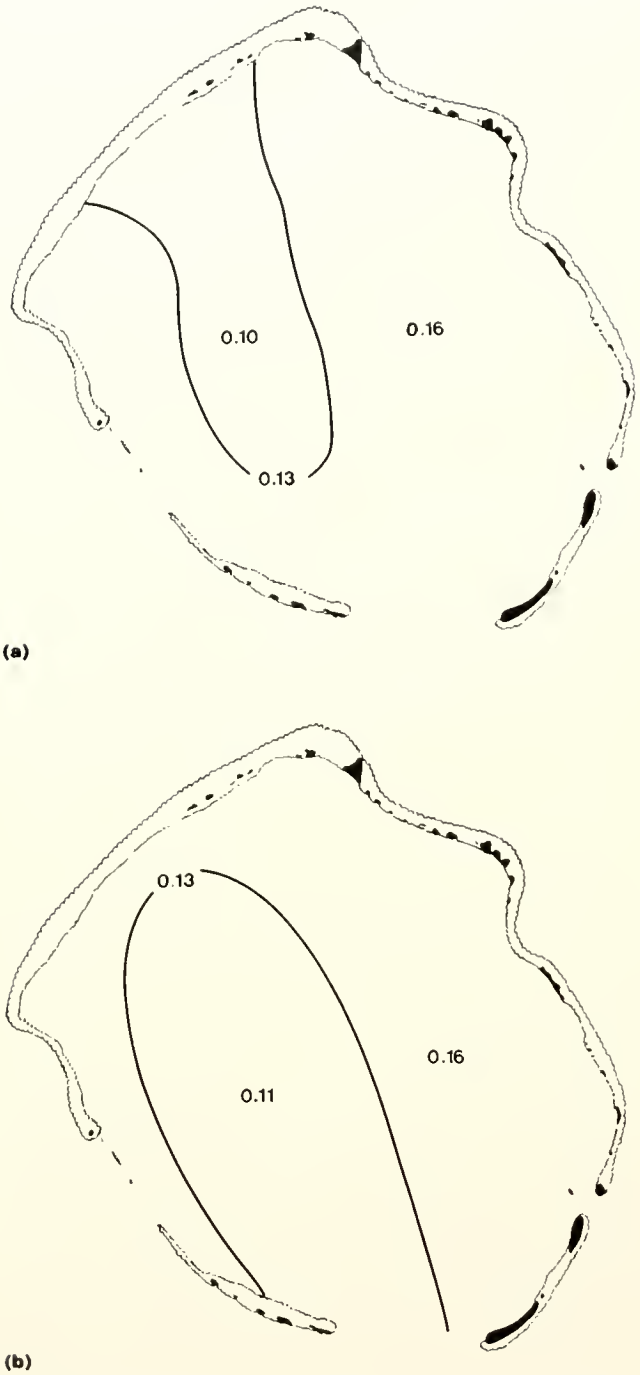

Fig. 3 Phosphate (a) and nitrate (b) contours for lagoon water. Concentrations in mmole m^{-3}.

windward cross-reef currents is shown in Fig. 2 by horizontal lines along the eastern boundary of the atoll. These currents are a result of breaking waves on the windward reef; they vary in response to surf height (and therefore regional wind patterns) and tide height. From Enjebi to Enewetak Island (Fig. 2), water crosses the reef from the ocean to the lagoon in a direction approximately perpendicular to the reef front. The windward cross-reef currents do not reverse direction, flowing from lagoon to ocean. The current speed ranges from 10 to 150 cm s^{-1}. These currents range in volume transport from 0.05 m^3 s^{-1} per meter of reef front during low tide and low surf to about 1.5 m^3 s^{-1} during high tide and high surf. A mean volume transport value of 0.56 m^3 $s^{-1}m^{-1}$ was calculated; this is equivalent to 6.6×10^8 m^3 per tidal cycle across the windward reef (a tidal cycle is used to facilitate comparison with other volume transports). The volume transport of the entire windward cross-reef current probably varies by a factor of 2 to 3. Winter tropical storms drive water over the reef in massive amounts, building and eroding atoll islands.

The area of leeward cross-reef currents is represented by vertical lines in Fig. 2. These currents do not flow in any well-developed pattern. Transport along the leeward reef, rather than across it, is common. During a period of high surf from a north swell, S. V. Smith and E. D. Stroup (January 1976, unpublished data) measured inward flowing currents along the northwest leeward reef. Current speeds and volume transports at 10 different locations ranged from about 15 to 50 cm s^{-1} and from 0.15 to 0.57 m^3 $s^{-1}m^{-1}$, respectively. Significant inflowing and outflowing currents were measured in the region north of Kildrenen Island and south of the Southwest Passage (Fig. 2). Noshkin et al. (1974), using surface concentrations of ^{238}Pu, ^{239}Pu, ^{240}Pu, and ^{137}Cs, have also shown that, during winter high tide periods, significant amounts of oceanic water enter the lagoon across the northwest and southwest leeward reef.

Dye releases on the leeward reef flat demonstrate a slow drift either oceanward or lagoonward over the leeward reef margin. A maximum value for oceanward flow might be the speed of the net oceanic drift of the lagoon surface current. A characteristic current speed over the entire leeward reef might be about 50% of the lagoon surface current speed. Much of the reef margin bares at low tide, so an estimate of the average depth of the reef is near 50% of the mean tidal range, or 0.42 m. The net transport of water out of the atoll over the leeward reef margin is estimated to be 0.4×10^8 m^3 per tidal cycle (i.e., only 6% of the windward reef input).

Channel Currents

The Deep Entrance current (Fig. 2) reverses approximately every 6.2 hours, with the tide. The current speed ranges from 0 to 80 cm s^{-1}, increasing from zero to a maximum in about 3 hours and decreasing to slack water in another 3 hours. The period of slack water in the channel is no more than a few minutes. The direction and speed of the current are nearly constant throughout the water column. The volume transport of the Deep Entrance current varies between neap and spring tides. On May 31, 1979, near maximum spring tide, the current transported 3.0×10^8 m^3 per 6.2 hours over an entire tidal cycle.

Surface and deep drogues placed in the channel on a flooding tide reversed on the ebbing tide and returned to near their original position. It was estimated that the net volume transport of the Deep Entrance is approximately zero over a tidal cycle.

The South Channel (Fig. 2) has a nearly continuous outflow. During flood tide, surface water drifts westward across the channel; on ebb tide, the surface current turns from westward, to southwest, to south. The surface water in the South Channel tends to move westward as wind drift, while water below a depth of 5 m moves southwest to south, depending on the tide condition. The current speeds range from 8 to 30 cm s^{-1}. Based on 20 drogue measurements and dye releases over a complete tidal cycle, the average outflow was estimated to be 6.9×10^8 m^3 per tidal cycle; this represents 75% of the total lagoon surface current volume transport and 105% of the estimated water flowing inward over the windward reef flats (Table 2, and material presented later).

The Southwest Passage is a shallow break in the leeward reef, yet it has a reversing current similar to the Deep Entrance (Fig. 2). The calculated volume exchange between ocean and lagoon is approximately 0.8×10^8 m^3 per tidal cycle. Because the currents are reversing (see previous discussion), the net outflow through these channels is small in terms of the water budget. The calculation of volume transport of water over the entire leeward reef includes this net outflow through this passage.

Lagoon Currents

Currents of the central lagoon may be characterized by a surface current, a mid-depth current, and a deep current. The currents are distinguishable by their characteristic speed and direction. The water column in Enewetak Lagoon is nearly isohaline and isothermal; salinity ranges 0.20 $^{0}/_{00}$ at most (average near 34.4 $^{0}/_{00}$), and temperature varies by no more than 0.5°C (annual range, 27°C to 29°C).

The surface current is wind-driven. The general surface drift is southwesterly, or downwind (Fig. 4). The spatial and temporal variations in the current directions are considerable. In the central lagoon, drogues move south, west, and north, appearing to respond to the wind direc-

TABLE 2

Water Budget; Estimates of Mean and Range

Current	Transport (range) 10^8 m^3 per 12.4 hour (+ is to lagoon; − is from lagoon)	Bases for calculation	Comments on current
Windward cross-reef	+6.6 (+2.2 to +19.8)	0.56 $m^3 s^{-1} m^{-1}$ reef front 27,000 m open reef front	June 21–29, 1971 continuous inflow.
Leeward cross-reef	−0.4 (0 to −0.8)	0.05 m s^{-1} 0.4 m (half tide range) 47,000 m open reef front	Variable flow. None to fast channel currents.
Deep Entrance	Net = 0 (−1.0 to +1.0) (3.0×10^8 m^3 transport each way)	0.40 m s^{-1} 34,000 m^2 (cross-sectional area)	Reversing. Typical tidal currents 0 to 0.80 m s^{-1}
South Channel	−6.9 (−4.5 to −8.5)	0.15 (0.07 to 0.23) m s^{-1} 145,000 m^2 (cross-sectional area) $(2/2)^{1/4}$ (conversion to normal direction)	Pulsing, continuous outflow.
Southwest Passage	Net = 0 (−0.2 to −0.2) (0.8×10^8 m^3 transport each way)	0.40 m s^{-1} 9,000 m^2 (cross-sectional area)	Reversing. Typical tidal currents.
Surface	9.2 (3 to 30)	0.06 m s^{-1} 10 m × 34,600 m (maximum cross-sectional area at 5 m depth)	Variable. Functional to wind speed.
Mid-depth	8.6 (unknown)	0.03 m s^{-1} 20 m × 32,000 m (maximum cross-sectional area at 20 m depth)	Variable. Functional to wind speed.
Deep	2.2 (unknown)	0.01 m s^{-1} 18 m × 28,000 m (maximum cross-sectional area at 39 m)	Variable. Functional to windward cross-reef input

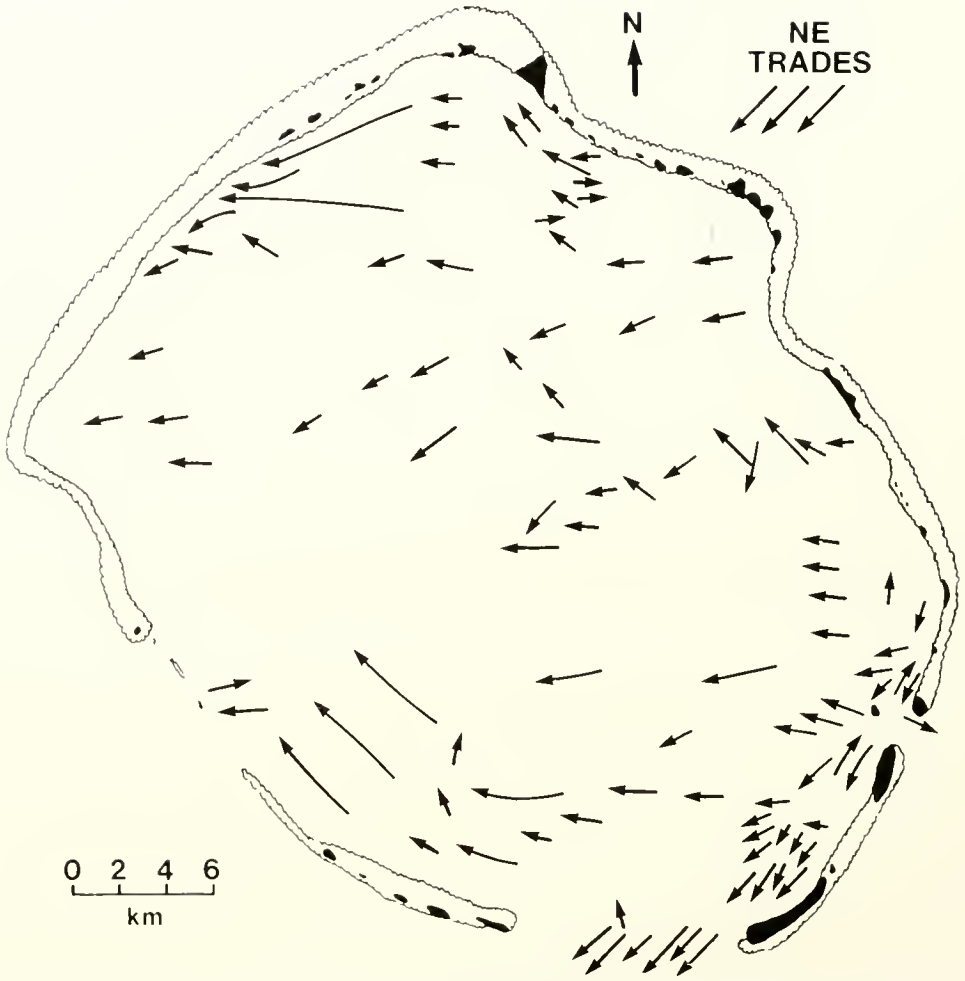

Fig. 4 Lagoon surface currents from drogue data. Arrows represent smoothed drogue trajectories over varying lengths of time; they are not vectors. Some drogue runs were made during calm or variable wind. [From Atkinson et al. with permission.]

tion of the previous 6 to 12 hours. Drogue paths over 6 hours showed no rapid changes in directions; however, they often traced slight curves, suggesting they were slowly changing direction with the wind.

The speed of the surface current is approximately 2% of the wind speed (Fig. 5). Data for Fig. 5 were taken from days when both the average wind direction and the average wind speed had small standard deviations. Correlations between wind and current speed and wind and current direction for all data are poor, probably because cross-reef currents and tidal channel currents influence the surface current at least 5 km into the lagoon.

The surface current moves in a layer which varies from 5 to 15 m thick. The average thickness of the surface layer is approximately 10 m. Downwind volume transport of the surface layer is approximately 9.2×10^8 m^3 per tidal cycle (Table 2). Von Arx (1948) reported that the surface current at Bikini is 5 to 20 m thick and changed depending on the wind conditions.

The mid-depth current lies between 10 and 30 m in depth. This current generally flows northeastward, oppo-

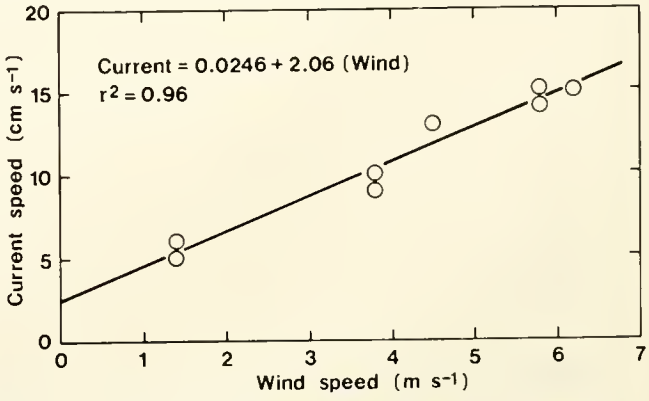

Fig. 5 Surface current speed as a function of wind speed for the center of the lagoon.

site the surface flow, at speeds of 2 to 4 cm s^{-1}. The volume transport of this current is approximately 8.6 $\times$ 10^8 m^3 per tidal cycle (Table 2).

The deep current flows southward between 30 and 50 m. This current is slow, ranging from 0.5 to 1.5 cm s^{-1}. Drogues in this current were followed for up to 10 days; while the cumulative direction and speed were consistent and predictable, a 6- to 12-hour east–west variability ("slosh") was noticed in their movement. This motion was attributed to flow around the lagoon pinnacles and/or tidal pulsing. The volume transport of the deep current is approximately 2.2 $\times$ 10^8 m^3 per tidal cycle through a cross section near the middle of the lagoon (Table 2).

Vertical Current Profiles in Lagoon

Figures 6a and 6b are photographs of vertically suspended fluorescine dye dispensers. These profiles reveal the spiral current structure of the lagoon water. The profiles show that the deeper currents are offset to the right (clockwise) from the shallower currents. Figure 7 is a graphic summary of the vertical dye profiles in the lagoon. The number at the end of each arrow is the depth in meters of the observation. The arrows have no magnitude because current speeds were not determined. In all stations across the lagoon, from Runit to West Spit (Fig. 7), the current spiraled to the right, forming a substantial eastward flow which is referred to as the mid-depth current. At two stations, deep scuba dives were made to verify the southern flow of the deep current previously documented with the deep current drogues.

Figure 8 is constructed from all the deep-drogue measurements and selected surface-drogue measurements made during the summer and winter periods. These data points represent end points of current vectors emanating from the origin. The shaded spiral indicates the resulting current structure. There are not sufficient data to resolve the spiral more accurately. The spiral reveals the basic three-current system: the surface current (0 to 10 m) is southwesterly, the mid-depth current (10 to 30 m) is northeasterly, and the deep current (30 to 50 m) flows southward.

The vertical current structure, as summarized by Fig. 8, can be altered by the cross-reef currents and tidal currents. The diagonal lines in Fig. 9 delineate the area of the lagoon directly affected by the windward cross-reef currents. At the northern end of the lagoon (region 1 in Fig. 9) these currents follow the contour of the atoll. Along the central part of the windward back-reef (region 2) the current may be going north, west, or south, depending on the tide and surf conditions. Near Enewetak Island (region 3) the current also follows the contour of the atoll. The surface current and deep currents in regions 1 and 2 move in the same direction when large volumes of water cascade over the reef. During spring low tide, however, when little water enters the lagoon over the reef, a surface current, mid-depth current, and deep current characteristic of the open lagoon can be observed (Fig. 7).

The currents directly behind the windward reef are variable in speed, being fastest when large surf drives water into these regions. Figure 10 is a plot on two successive days, showing the current increase with rising tide. Notice that the second date had higher surf and a slightly higher wind speed than the first date. The two linear regression coefficients are significantly different at the 95% significance level. These data were taken at the site denoted "A" in Fig. 9.

The cross-hatched areas in Fig. 9 delineate water that experiences reversing current through the Deep Entrance and the Southwest Passage. The area near the northwestern leeward reef, marked by circles in Fig. 9, is an area of convergence. The lagoon surface water cannot escape over the leeward reef, particularly when large surf drives oceanic water over these reefs into the lagoon. Large aggregations of jellyfish have been observed in this region, as well as strong southwesterly flow along the lagoonward margin of the reef.

WATER BUDGET

Table 2 is a summary of the volume transports for the important components of the water budget.

Input

The water can flow into the lagoon from the windward reef, the Deep Entrance, and the Southwest Passage. The windward cross-reef current transports about twice as much water as the Deep Entrance current. Because the windward cross-reef current never reverses, the volume transport over the windward reef represents net input of water into the lagoon. The Deep Entrance and the Southwest Passage show net transports of approximately zero over each tidal cycle.

Output

The water can flow out of the lagoon from the leeward reef, the Deep Entrance, and the Southwest Passage. Because the Deep Entrance and the Southwest Passage have net transports near zero over each tidal cycle, the net inflow from the windward reef must exit as outflow over the leeward reef and out the South Channel. Because the flow over the leeward reef is relatively small (Table 2), most of the water flows south, exiting out of the South Channel.

The numbers in Table 2 do not sum to zero over a tidal cycle; however, these data were collected during different tide stages. Ranges were included in the table to indicate the natural variability of the system.

CIRCULATION MODEL

Lagoon circulation can be explained as a response to three sources of energy: (1) the surf on the windward ocean reef, (2) the wind, and (3) the tides.

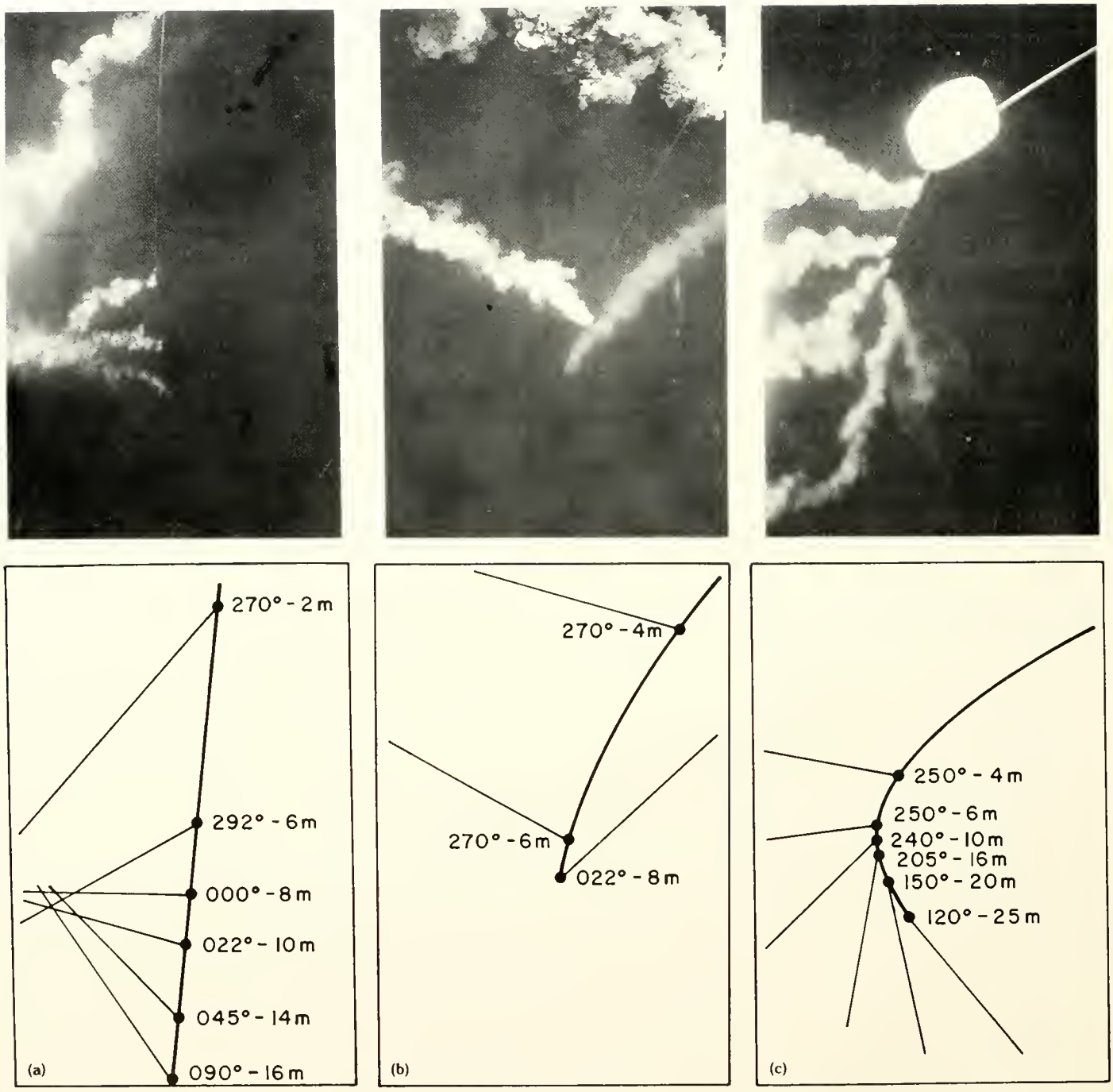

Fig. 6 Photographs a and b show right-handed vertical current profile. Photograph c shows the left-handed vertical current profile 2 km north of Enewetak Island. Direction of current and depth of dye dispenser are shown in the line drawing below the photographs. See Fig. 7 for location. [From Atkinson et al. with permission.]

Surf

The breaking waves on the windward reef drive water over the windward reef flat and into the lagoon primarily on the eastern (prevailing windward) side of the atoll. The cross-reef currents and the currents behind the reef are, therefore, dependent on the surf height and the depth of water on the reef. This oceanic water spreads into the lagoon, moving downwind and mixing vertically and horizontally. Since the South Channel is the only significant region of outflow, the water column has a net transport to the south. This southerly net volume transport must

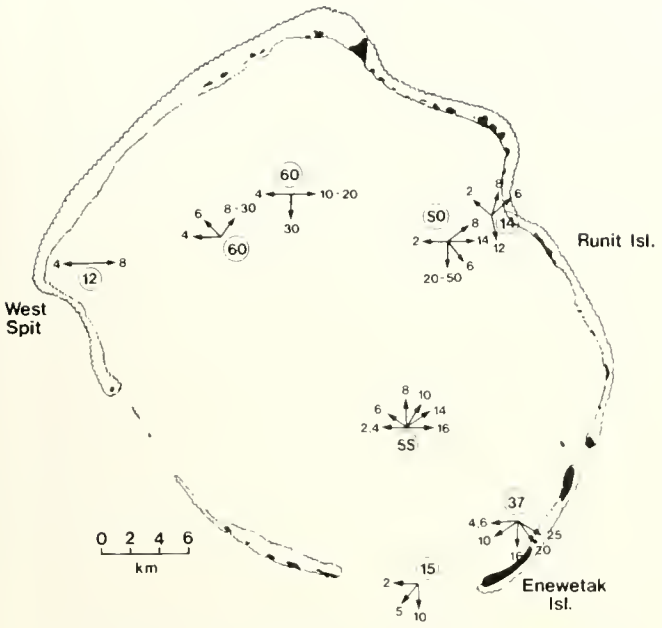

Fig. 7 Vertical current profiles. Number at end of arrow gives depth in meters. Arrow gives direction of the current. Circled number gives the depth of the bottom in meters. [From Atkinson et al. with permission.]

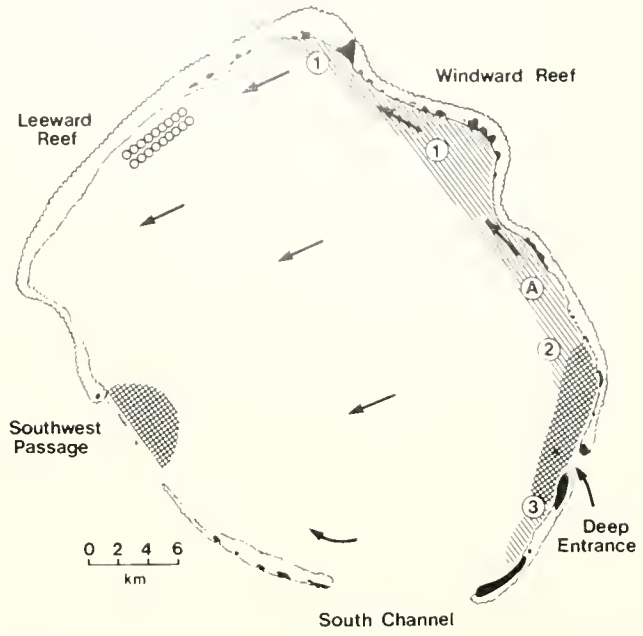

Fig. 9 General current patterns in the lagoon. See text for key.

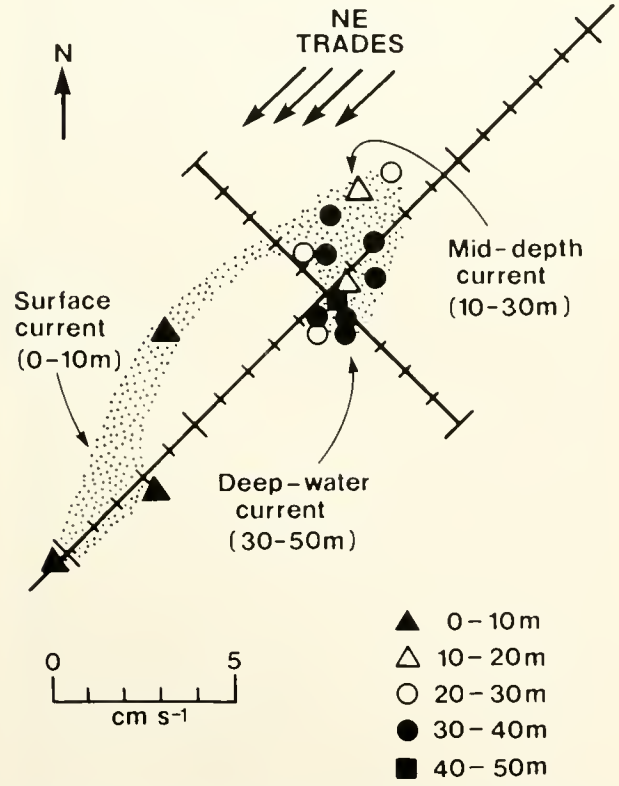

Fig. 8 Summary of drogue results. The shaded spiral represents the approximate endpoints of current vectors from the origin. [From Atkinson et al. with permission.]

increase toward the south end of the atoll to accommodate the inflowing water across the windward reef. Figure 11 shows the relative increase in southerly volume transport versus distance from the north end of the atoll. These relative volume transports are based on cumulative transport across the windward reef. These are reported as relative values, since variation in swell and wind direction alter this relationship an unknown amount.

Wind

The wind creates the downwind drift of the surface water and the upwind drift of the mid-depth water. These can be qualitatively described as a special case of Ekman wind-driven circulation. This pattern is superimposed on the net drift of the entire water column toward the South Channel. This southerly drift can be observed in the deep water, below surface layers affected by the wind.

The northern end of the atoll has a relatively small southerly drift based on cumulative net input (Fig. 11); therefore, the effect of the wind can be observed at a deeper depth in the north end than in the south end of the atoll. Drogues suspended at 38 m in the north end moved northeast to east, whereas drogues at a similar depth in the southern end moved south. The increasing volume transport from north to south, due to the increasing net input over the windward reef, creates a southerly deep current that thickens toward the southern end of the lagoon. Figure 12 is a plot of the 38 m drogue directions versus distance from the north end of the atoll. By the middle of the lagoon, the layer at 38 m is well within the southerly deep current (Fig. 12).

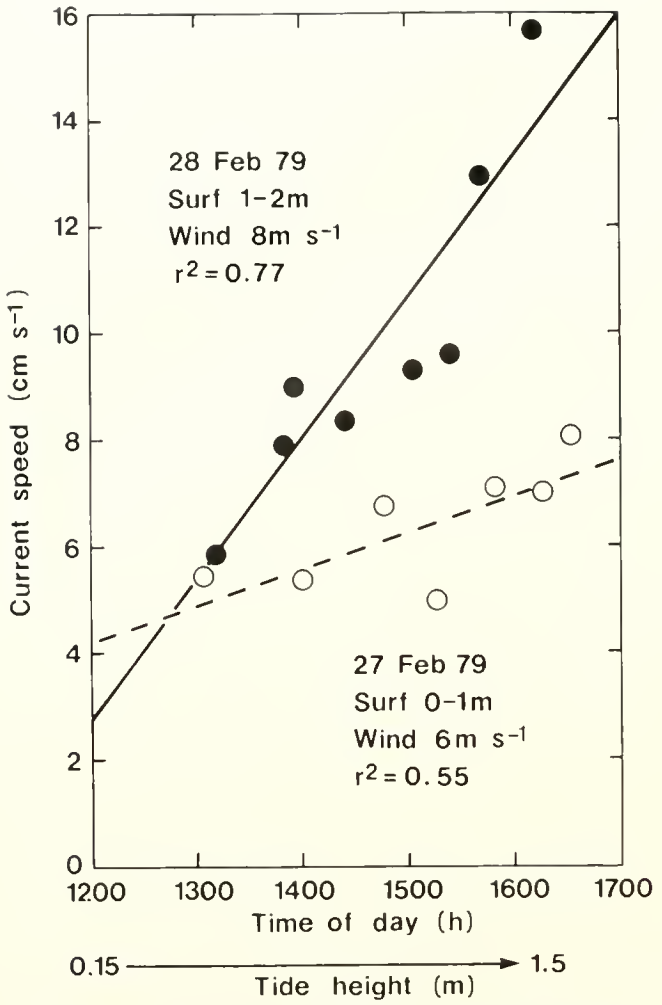

Fig. 10 Change in current speed as a function of tide height near Runit on successive days. Average current speed plotted at midpoint of time interval.

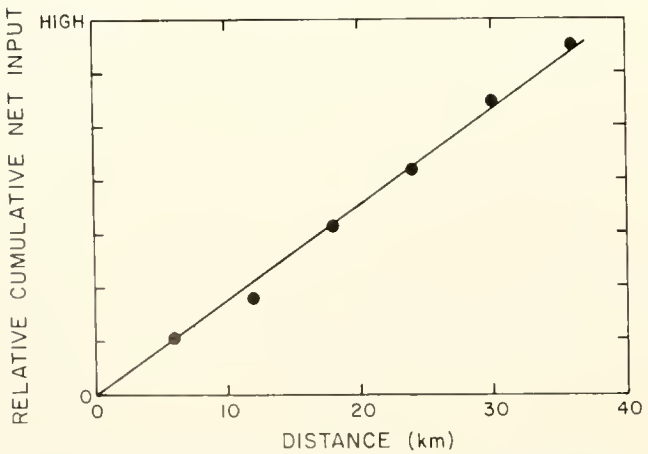

Fig. 11 Increase in cumulative net input over the windward reef flat as a function of distance from the north end of the lagoon.

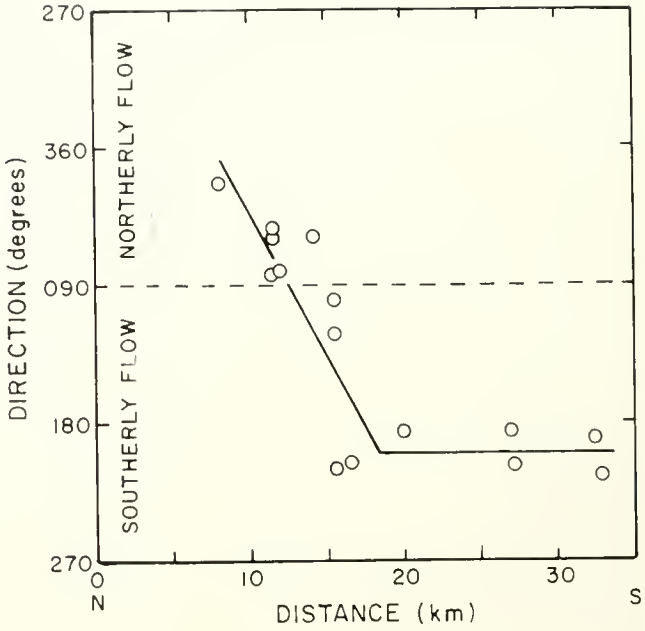

Fig. 12 Change in direction of drogues suspended at 38 m as a function of distance from the north end of the lagoon.

The observed pattern of wind-driven currents resembles in many ways the pattern predicted by Ekman for an enclosed sea in which the following conditions apply: (1) impermeable, closed boundary; (2) constant, unidirectional windstress over the entire surface; (3) homogeneous water; (4) uniform depth; and (5) constant eddy viscosity. At Enewetak these conditions are only partially met. The lagoon rim is closed neither to leeward nor windward; in particular, large quantities of water are introduced along the windward edge (Table 2).

In a fully enclosed sea, the Ekman flow integrated over depth is zero at every point. In a lagoon such as Enewetak this will not be the case, but the detailed effects of the "leaky" boundary and the irregular bathymetry have not been estimated from present data. The remarkably shallow spiral pattern of currents is a new finding which should be further investigated and modeled.

Surface current speeds are 5 to 20 cm s^{-1}, approximately 2% of the wind speed. The surface drift is generally downwind and seems responsive to the wind direction of the previous 6 to 12 hours. The mid-depth upwind current speeds are about one-half of the surface current speeds.

These wind-driven currents would cause the surface water to overturn in 5 to 10 days if there was no vertical mixing. Von Arx (1948) estimated approximately the same time for turnover at Bikini. Von Arx (1949), Munk et al. (1949), and Ford (1949) suggested that the surface water at Bikini sinks in the western portion of the lagoon and upwells in a small band in the eastern portion of the lagoon. No direct evidence of upwelling has been found at Enewetak. Upwelling, if it exists as such, will be largely intermittent, because of the intermittent (tidal) pulsing of

the windward cross-reef inflow of surface water. At a maximum (high tide, active surf), this inflow is approximately equal to the downwind transport of the lagoon surface layer; during these intervals, upwelling is not required by continuity to supply the wind-driven surface transport. The essentially vertical homogenous water in Enewetak Lagoon suggests that surface water mixes with bottom water before reaching the leeward side. It also does not allow any conclusions regarding the presence or absence of upwellings from distributions of water properties. At Bikini, Ford (1949) was able to follow the motion of discrete water distinguished by salinity variations.

Surface, mid-depth, and deep water salinities at Enewetak are shown in Figs. 13a, b, c. These salinity contours show some of the general features of lagoon circulation. Surface water was slightly less saline than deep

Fig. 13a, b, c Salinity for surface (0 to 10 m), mid-depth (10 to 30 m), and deep (30 to 50 m) water. (Collected by S. V. Smith, July 26 to Aug. 16, 1974.)

water because the weather was rainy during the collection period. Relatively high salinity ocean water cascades over the windward reefs and flows in through the Deep Entrance.

Northeast trade winds blow less saline surface water downwind with a buildup in the northwest region of the lagoon. Because water is trapped in the leeward side of the lagoon, return flow develops in the deeper water. The low salinity return flow is mixed with surface water, creating a relatively vertically well-mixed water column with low salinity downwind and high salinity upwind. During long dry periods, opposite salinity gradients might be expected, with high salinities downwind and relatively low salinities upwind. Only a small portion of downwind surface water escapes out of the Southwest Passage. The excess water must move south toward the South Channel; consequently isohalines bend toward the south (Fig. 13). There is no evidence of a discrete water mass sinking on the downwind side of the lagoon, flowing upwind as deep water, and upwelling on the leeward side of the lagoon (as reported by Ford, 1949 at Bikini). The water column appears vertically well mixed (Table 1 and Fig. 13). There is also no suggestion that water can maintain vertical structure for 5 to 10 days at Enewetak. As ocean water pours over the windward reefs and into the lagoon, it mixes vertically and horizontally as it moves downwind. Consequently the salinity gradient is low to high, west to east, regardless of depth. The water on the windward side of the lagoon is predominately ocean water, but water on the western side of the lagoon reflects net processes in the lagoon. Scuba divers can observe strong mixing on the upper vertical wall of the West Spit. Lower salinity lagoon water mixes with high salinity ocean water in this region. Phosphate and nitrate are lower in the western lagoon water than in eastern water. Because water on the eastern side in general reflects net lagoon processes, low nutrients in that water suggest net uptake of these nutrients into the ecosystem. Net organic production of benthic ecosystems has been estimated by net uptake of nutrients (Smith and Jokiel, 1976; Atkinson, 1981; Smith and Atkinson, 1983). The observed decrease in these nutrients indicates a reasonably low, net organic production for the atoll.

Ford suggested oceanic eddies might move through the broad open channel at Bikini, the Enyu Channel. Perhaps this process might occur in open lagoons; however, it does not appear to occur at Enewetak. Large eddies would be destroyed when flowing into the lagoon by strong tidal currents in the channels. Although a large eddy could not be maintained, large oceanic eddies moving by the atoll could influence the chemical and biological composition of inflowing water.

Tide

Tidal currents directly influence the flow of water within several kilometers of the passes, especially in the southern part of the lagoon. These tidal currents can overwhelm the wind-driven circulation, leading to such local effects as the "left-hand" spiral observed two kilometers north of Enewetak Island (Fig. 6c).

RESIDENCE TIMES

In the most elementary analysis, the average residence time of water in the lagoon can be estimated by dividing the lagoon volume by the net rate of water input. The calculation yields a residence time of 33 days. Clearly there is a variation of actual residence time from one part of the lagoon to another because: (1) the water is introduced all along the windward reef, but exists primarily through the South Channel; and (2) there is no major north–south recirculation mixing northern waters with southern water. Thus, the residence time for water entering the north end of the lagoon will be relatively long; water entering across the southern reef will have a short residence time.

Because the water entering the northern lagoon must transit the entire lagoon before exiting and because it undergoes mixing by the superimposed wind-driven circulation during that transit, a very simple estimate of the residence time for that part of the inflow will have at least qualitative validity. If it is estimated that the northern part of the lagoon receives one-quarter of the total inflow, then the residence time for this water (under the same very simple assumptions) will be four times longer than that for the lagoon water as a whole, or 132 days.

Water entering the system in the north is of particular interest because it flows across the areas with high bottom-sediment concentrations of transuranic radionuclides (Nelson and Noshkin, 1972). Figure 14 is a generalized plot of sediment radionuclide activity; it indicates that if release into the water column is proportional to the concentration in the sediment then most of the radionuclides

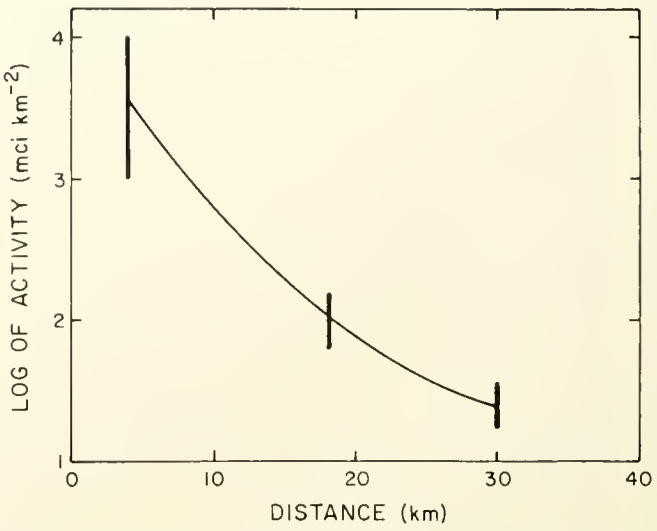

Fig. 14 Decrease of sediment radionuclide activity as a function of distance from the north end of the lagoon. Radionuclides include ^{90}Sr, ^{239}Pu, ^{137}Cs, ^{60}Co.

are released into northern lagoon water, which has residence times well above the average for the whole lagoon. The concentrations of radionuclides in the water column decrease from the northern end of the atoll to the southern end, by a factor of 2 to 5 (Noshkin et al., 1974). This horizontal gradient reflects the general increase in flushing rate in the south end of the lagoon, as well as horizontal diffusion from the north end.

The water column is vertically well mixed in terms of temperature and salinity. However, in the central lagoon the horizontal diffusion rates for certain materials may be greater in the surface water than in deep water. Near the windward reef, where both surface and deep currents respond to the cross-reef currents, vertical transport may be greater than in the central lagoon, and there may be no difference in horizontal diffusion rates between surface water and deep water.

VON ARX MODEL FOR BIKINI

Von Arx's (1948) model conceptualizes lagoon circulation by linking two basic patterns: a "primary circulation" and a "secondary circulation."

The primary circulation consists of wind-driven surface water moving downwind, sinking, and then returning upwind to the windward (eastern) side of the atoll lagoon as deep water.

The secondary circulation consists of horizontal recirculation of deep water. Von Arx reported that the volume transport of the eastern flowing deep current is greater than the volume transport of the surface current. He concluded that some of the deep water is shoaled upward or "upwelled" in the eastern part of the lagoon, becoming the surface current. The remaining portion of the deep water diverges at the leeward edge of the windward reef. Some water moves northward following the bathymetric contour of the basin. The deep water circulation forms two counter-rotating bodies of water, the northern one moving counterclockwise and the southern one moving clockwise.

Von Arx estimated that the exchange of lagoon water through all channels and passes during winter is approximately 3.8% of the total lagoon volume per tidal cycle. At a 30% exchange efficiency, von Arx estimated the winter Bikini lagoon flushing to be 39 days. The summer flushing time was estimated to be twice as long as that in the winter.

The conspicuous feature of von Arx's model for deep atoll lagoon circulation is the deep return flow toward the windward side of the atoll. This return flow connects the primary circulation with the secondary circulation. The model for the circulation system of Enewetak has some similarities to the model proposed by von Arx for Bikini. The primary circulation system consisting of an overturning wind-driven surface current is the same in terms of speed and volume transport.

The secondary system, or deep circulation, is not the same as that proposed by von Arx. The deep current at Enewetak flows southward, toward the channel having net outflow. Von Arx described a horizontally recirculating deep current with a volume transport greater than the surface current, hence upwelling on the windward side. At Bikini the large open channel (Enyu Channel) is at the southeastern end of the lagoon. A net transport toward this channel would create an eastward flowing deep current. The eastward mid-depth current and the "passward" deep current would then appear to be a single deep current with a mass transport greater than the surface current. The excess volume transport of von Arx's deep current might largely be balanced by net outflow through Bikini's southeastern channel. Von Arx did not report a large net outflow; however, recalculation of his data suggests net outflow through the Enyu Channel. Outflow was also shown in the distribution of indigenous zooplankton (Johnson, 1949) and was observed in surface radionuclide patterns (Noshkin et al., 1974). To reach the Enyu Channel, the deep water in Bikini Lagoon must move eastwards. In Enewetak Lagoon the only effective exit is at the southernmost part of the atoll; therefore, the deep water must move southward.

Note that in the model derived from Enewetak, the deep motion is primarily controlled by the location of the major exit points from the lagoon. Water flow through other atoll lagoons seems to be regulated by atoll morphology and local wave and tidal conditions (Milliman, 1967; Gallagher et al., 1971; Henderson et al., 1978; Ludington, 1979). Studies of deep currents in other deep lagoons could be valuable in testing this interpretation.

CONCLUSION

Windward and leeward cross-reef currents, channel currents, and tidal flow are the major factors influencing the exchange of water between atoll lagoons and the surrounding ocean. Because these factors are specific to local wave climate, tidal conditions, and atoll morphology, atoll lagoons have widely varying flush characteristics. Wind-driven circulation, a pervasive feature of lagoons, contributes primarily to internal circulation rather than flushing. Upwelling on the windward side of lagoons may occur as a summation of the above phenomena but does not seem to be a generalizable feature of deep lagoon circulation. Deep water flow appears to orient itself toward the channels of net water output.

ACKNOWLEDGMENTS

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Chapter 6

Meteorology and Atmospheric Chemistry of Enewetak Atoll

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INTRODUCTION

The Marshall Islands area has a marine climate that varies from tropical to subtropical; near Enewetak Atoll the weather is characterized by brisk steady winds, moderate rainfall, and unvarying high temperatures with typical partial cloudiness. The atoll lies near the northern edge of the tropical zone dominated by the migrating equatorial trough of low pressure, with its heavy rains. It lies well within the northeast trade wind area of the North Pacific; that is, the surface winds are from the east and northeast on average. There have been more than 20 years of careful meteorological observations at the airstrip on Enewetak Island, and we make use of some of the archived data to discuss, in turn, the various aspects of the weather. In the section on climate and weather, we cover briefly the mean and variation for each observed quantity of interest and note our state of knowledge of these factors. Also in that section we set out an annotated bibliography of sources of additional data and of specialized discussions. In the section on the atmospheric chemistry of the atoll, we make use of the extensive data collected during experiments there in 1979.

We discuss both the mean value and expected range of variation because neither alone covers all of the weather. The variability of the weather is the combined effect of disturbances of various scales which may have well-defined structures in space and time and of phenomena that can be taken as random. We begin by discussing some of the more common structured disturbances. Over the years diurnal variations at island sites have been discussed and analyzed. While there is no doubt that there are diurnal cycles in cloudiness and precipitation, no attempt is made here to provide explanations for them in terms of first causes because the interaction can be both subtle and complex. Also, at short periods there is the atmospheric tide, primarily a thermally driven effect that produces global pressure fluctuations and wind patterns that are rather complex. The influence of the atmospheric tide at the surface, though greatest in the tropics, is relatively small, and we mention it only briefly. The semidiurnal fluctuation is the dominant mode of the tide and has an amplitude of about 1 mbar, or 85% of the diurnal variance about the annual mean of 1010 mbar pressure at Enewetak. Chapman and Lindzen (1970) developed the presently accepted theory of the tide. The discussion by Lavoie (1963) of calculations available at that time is superseded, despite the absence of seasonal effects in Chapman and Lindzen's basic model. Nevertheless, the data presented by Lavoie for the monthly variation of tide parameters are correct and illustrative, despite the relatively short record.

Disturbances lasting a day or more are common in the tropics, and we discuss them in the sections entitled "Tropical Storms and Disturbances" and "Winds Aloft." There are two seasons at Enewetak, the dry season from December through March and the wet season from April through November. Annual variation is crucial to understanding the weather in the tropical marine environment, and this influence is included in each section, particularly in the section on precipitation.

Although there has been much work recently on the variability of climate over periods of a year to a decade, we cannot say much yet about how such changes affect the tropical islands. It is known that there are quasi-periodic fluctuations in the strength of the Pacific trade winds correlated with equatorial sea surface temperature variations at very large scales and that there follows a chain of consequences that includes changes in both tropical and mid-latitude circulations. A clear exposition on this subject, the Southern Oscillation, is to be found in Trenberth (1976). While much of the present interest stems from the possibility that disturbances in mid-latitude weather and coastal upwelling could be forecast months ahead, we will certainly learn much about the tropical climate itself from the numerous studies now under way.

CLIMATE AND WEATHER OF ENEWETAK ATOLL

Temperature and Humidity

It is obvious that high surface temperature and humidity are to be expected on tropical islands. It is less obvious, but well documented, that it is difficult to obtain accurate temperature measurements in an operational program in such environments because of such factors as radiational heating of the shelter in daylight. Thus it is likely that the air temperature range reported below is exaggerated by about 0.5°C (see Lavoie, 1963, for a discussion). This is a small enough error for temperature, but it significantly degrades the accuracy of the relative humidity. Nevertheless, we can see that there is relatively little change in these quantities through the year and that a regular diurnal cycle is evident. The temperature and humidity both respond noticeably and regularly to rain showers, but in the data presented here the nearly random occurrence of rain with time has smoothed out this effect; in fact, even hourly data do not show the full effect of short-lived rain events.

The temperature and humidity data shown in Fig. 1a–c are from the U. S. Air Force measurements now archived by the National Climatic Center. Made at hourly intervals between 1945 and 1969 (with irregular breaks), the observations correspond to 14.1 years of uninterrupted measurement. This record is sufficiently long that the overall pattern and its variability can be perceived. The data averaged over 3-hour periods are displayed as a function of the hour and of the month; the draft plot is extended beyond the borders shown so that edge effects are minimized.

That the temperature depends very little upon the time of year can be seen in the mostly horizontal contours shown in Fig. 1a. Also note that the highest daily temperature is recorded between 12 and 15 hours local standard time and lies between 28.5 and 30°C; the lower temperature is observed in the dry season and the higher during the wet season. In the morning and in the evening, the temperature depends even less upon the time of year, with values increasing and decreasing daily through the upper 20s. In the hours after midnight, the decrease of temperature slows in the dry season and ceases in the wet season, with the lowest average value reaching 26 to 27°C.

Now these are monthly and 3-hour averages over years of data, and even though these patterns are generally valid, there are fluctuations. The representativeness of this pattern can be seen in the small variances: just over 0.5°C at night to a maximum of under 1.5°C in the afternoon in October. (These are variances of hourly data averaged over 3-hour periods for each month, i.e., variances about the mean shown in Fig. 1a.) This method of averaging does not accurately record the *average maximum* and *average minimum* hourly temperatures for each day. These are given in Table 1 for each month of the year. The range of temperature is greater here, as expected. The average minimum temperature for each month is nearly independent of month at about 23°C, whereas the average maximum exceeds 32°C in August and September and is 30°C during the dry season.

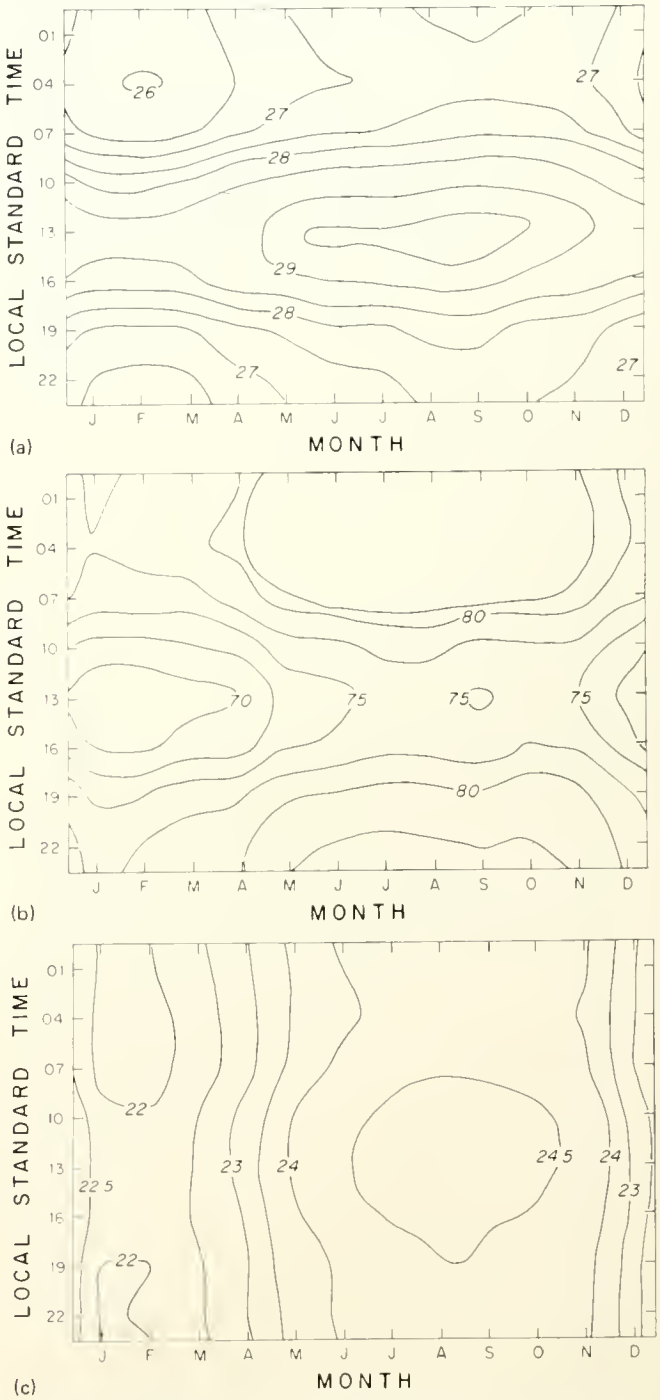

Fig. 1 Temperature and humidity data for Enewetak. (a) Dry bulb temperature, °C; (b) Relative humidity in percent; (c) Dew point temperature, °C. These are three hour averages for each month. Contour interval is 0.5°C for temperatures, 2.5% for humidity.

TABLE 1

Average Minimum and Maximum Temperatures, °C

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Minimum	23.5	23.4	23.6	23.8	23.5	24.0	23.6	23.6	23.8	23.4	23.7	23.8
Maximum	30.4	30.5	30.6	31.1	31.4	31.6	31.8	32.3	32.3	32.1	31.7	30.9

Extremes of temperature have also been recorded but provide little additional information. The annual minimum value of 21°C has occurred once in the record and the maximum of 34.4°C three times. The values reported by Blumenstock and Rex (1960) are less reliable because of shorter records. As mentioned above, it is possible that the maximum temperatures are overestimated.

Similarly averaged relative humidity data shown in Fig. 1b exhibit a bit more time dependence than the temperature. There is a broad maximum in the early morning followed by decreasing values as the temperature rises in daylight. The afternoon minimum is lower but briefer in the dry season than it is in the wet season. These values are the best estimates available but may be underestimated during the day by several percent if the temperature is overestimated by 0.5°C. The dew point temperature—the temperature at which saturation will occur if the air is cooled—is less sensitive to such error and is a straightforward indicator of the moisture content of the air. The distribution shown in Fig. 1c seems quite different from, but is entirely consistent with, the data in Fig. 1a and b. The dew point temperature is strongly dependent upon the time of year, with a broad minimum in the dry season and a broad maximum in the wet season. In both cases there is an increase during the daylight hours. This increase represents a slight increase in the water-vapor mixing ratio, which is consistent with increased evaporation during the day. It is this increase which prevents the relative humidity from decreasing more than it does in the afternoon.

Precipitation

Across most of the North Pacific, including the Marshall Islands area, the rainfall increases markedly from mid-latitudes to just north of the Equator. At Wake (19°N) the annual total is 940 mm, at Kwajalein (9°N) about 2400 mm, and at Jaluit (6°N) it exceeds 4000 mm. The highest values are in the equatorial trough near 3° to 6°N and the lowest in the subtropical high pressure area at about 25°N, well east of the dateline. Enewetak at 11°N lies near the northern edge of the zone of most rapid decrease of rainfall with latitude. The average rainfall of 1470 mm is not distributed uniformly through the year; about 85% comes during the wet season, which starts in April and ends in mid-November. The variability of the rainfall is remarkable, and this factor is a central theme in the discussion which follows.

There is much contention in the meteorological literature over the applicability of island-based rainfall data to open ocean conditions. This is not an issue here as we are concerned with the rainfall *at* the atoll, not in the environment in its absence. We note briefly below the limited data available to discern gradients across the atoll.

The rainfall distribution through the year, which is based on the archived data tabulated by Taylor (1973), is shown in Fig. 2a. The three measures shown for each month are the rainfall amount exceeded in 90, 50, and 10% of the years. Thus the amount expected (50% occurrence) in November, about 124 mm, is somewhat less than the 140 mm in the "rainiest December in 10 years." It can be seen at once that in certain months there is a very large range of variability. Although the average April has about 40 mm of rainfall, one year in ten may have less than 10 mm; another may have over 260 mm. The record represented here is 32 years long; there are missing data, but 26 to 29 years of monthly values are available in the various months. A longer series would probably not change the annual total much, and because it is inherent in tropical rainfall, the fluctuation evident in Fig. 2a would not be reduced by additional years of observation.

For this discussion, we let the dry season begin with December. That this is arbitrary can be seen by comparing the 10% value in Fig. 2a for December with the 50% value for November and the 90% value for November with the 10% value for December. When the wet season ends early, the November rainfall is less than 120 mm, whereas when it ends late, the December total exceeds 50 mm. The January, February, and March 50% values all lie between 20 and 35 mm, and the 90% values are uniformly very small at <10 mm. Many of the dry season rain events are from small cumulus clouds; however, these affect the total amount less than the infrequent disturbances. We follow the usual designation and let the wet season begin in April despite the small increase in the 50% value; this may be rationalized by the jump in the 10% figure—i.e., some Aprils are very wet.

The increased rainfalls of May and June are followed by 50% values between 175 and 225 mm in July through September. The maximum is in October, which also has the highest average and the greatest 90% total. November is a transitional month. The number of days with measurable (>0.25 mm) rainfall is greatest in August at 21 on the average; this figure varies between 10 and 21 for the wet season months, while it is 10 to 15 during the dry season.

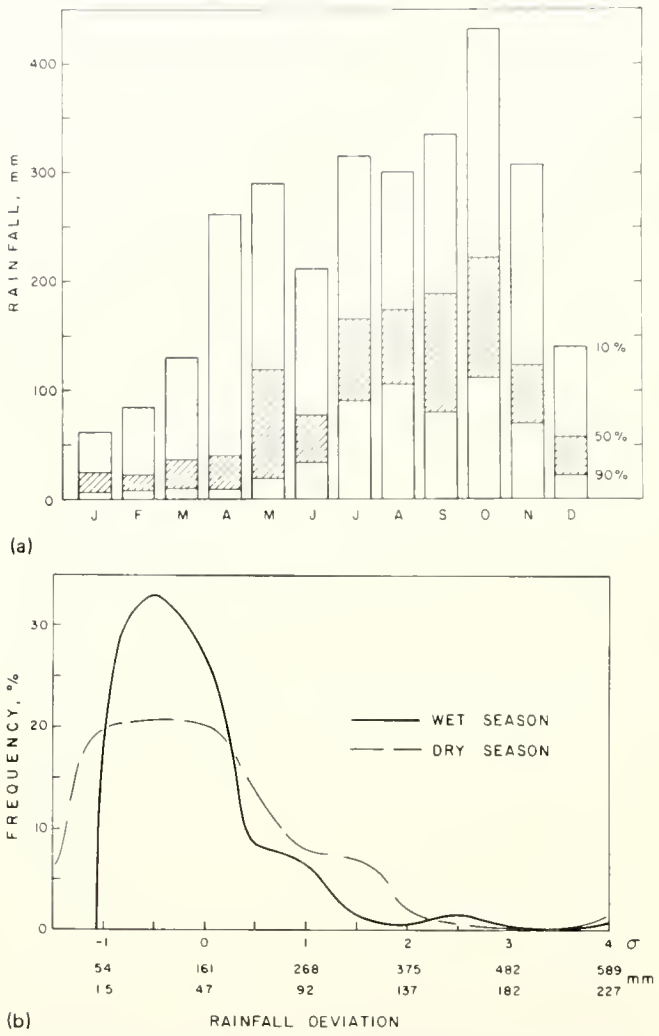

Fig. 2 Rainfall data for Enewetak. (a) Rainfall amounts for each month. The three measures correspond to the amount, in mm, exceeded in 90% (below shading), 50% (above) and 10% (top) of the months in the record. (b) Deviation frequencies for the wet and dry seasons. The curve shows the percent occurrence of deviations from the seasonal mean in units of σ, the square root of the variance. The corresponding rain amounts, in mm are shown below the axis.

Thus, as noted above, there are many small rain showers even in the dry season. The wet season amount includes such cumulus showers and a greater number of larger, sustained rainfalls during disturbances and during the infrequent tropical storm or approach of the equatorial trough; these are much less common in the dry season.

Another way to look at the variability of the precipitation is shown in Fig. 2b, where the frequency of occurrence of monthly amounts is given as a function of the deviation from the season average. Note first that in both regimes the most common value is significantly lower than the mean, about 0.5 σ below. (Here σ is the root mean square deviation of rainfall amounts for the season.) In the dry season, very dry months are common, but a few months with large amounts of rainfall do occur. For example, 2% of the years would be expected to have a "dry" month with 160 mm of rain, 2.5 σ above the average. Note also that the overall occurrence of the large rainfall months is not dependent upon the season but that the amount of precipitation is. The infrequent 3 or 4 σ cases for the wet season correspond to very substantial totals. These frequency distributions are typical of subtropical sites but are somewhat uncertain far from the mean value because of the limited length of record. Also, since these frequencies were averaged over the entire season, the month-to-month variation, which is large in the wet season, is lumped together with the interseasonal difference here.

Insufficiency of data limits one's ability to document diurnal variation in precipitation amount. Nevertheless, Lavoie (1963), using primarily Enewetak data, presented convincing evidence of an early morning maximum in frequency of rain; the deviation is perhaps 15% at the peak. There is some evidence in the same data set for a broad and weak afternoon minimum in the rain occurrence. Lavoie considered several mechanisms in an attempt to rationalize these values and to explain some significant difficulties: the data have large scatter, and even the maximum does not appear at every station. It thus seems best to say that there is a tendency for a maximum in the rainfall occurrence in the early morning and a weak minimum in the afternoon.

Even more limited are data giving the spatial distribution of rain about the atoll. Any variation is assumed to be primarily random because of the low relief of the atoll—i.e., the absence of orographic forcing. However, there could be sufficient disruption of the thermodynamic structure of the atmosphere by the presence of the lagoon to cause a discernable pattern. Data laboriously collected by Blumenstock and Rex (1960) for six special sites on islands around the atoll during 2-week periods, once in each season, have not to our knowledge been carefully analyzed in the literature. They reveal no systematic pattern of variation. The rainfall amounts at the various stations are highly correlated only when the stations are close together, and there is always some difference among them. The record thus appears consistent with rain areas of various sizes unforced by the atoll itself. Nevertheless, this does not rule out some such forcing in other circumstances. This record does not include any disturbed weather periods during which there could be a measurable difference of rainfall across the atoll.

Cloud Cover and Solar Radiation

Accurate estimates of cloud distribution and type are not easy to obtain, particularly at night and when low clouds obscure the sky. As discussed by Blumenstock and Rex (1960), there is likely a systematic bias—overestimation. Fortunately the overall cloud amount is least affected, and voluminous data exist for this quantity in the archive. Again, the average variation with time of day and time of the year is the main topic of discussion.

The fraction of the sky covered by clouds exceeded 75, 50, and 25% of the time as shown in Fig. 3, which is based on the tabulated three hourly frequencies of cloud cover in tenths.

The cloudiness is more variable in the dry season than the wet; indeed, the daytime sky is covered $^5/_{10}$ or more 75% of the time in July through October. More than $^9/_{10}$ cover is common (≥25%) in April through November, and this frequency does not depend upon the time of day. The expected cloudiness (i.e., the 50% value) varies from about $^5/_{10}$, higher in daylight and lower at night, in the dry season to about $^7/_{10}$, with somewhat less diurnal variation in the wet season. The sky is seldom clear, even in the dry season. Two-tenths of the sky is covered more than 75% of the time (although this may be biased at night).

A different measure of cloud cover is obtained from satellite observations. Images obtained routinely from geostationary platforms show the aerial extent and temporal evolution of cloud systems. In addition, radiometric measurements of the cloud top temperature yield good estimates of the cloud top height. Accurate measurements below obscuring layers of high clouds are not yet obtainable routinely.

We are not aware of any published solar radiation data for the Marshall Islands area, but there are data for certain times in 1977 to 1979 (see "Sources of Additional Data"). It is obvious that the typical partial cloudiness and the high moisture content of the near-surface air significantly diminish the incident sunlight. Working against this, however, is the long (and unvarying) day. The interval between sunrise and sunset varies from 11 hours 29 minutes to 12 hours 46 minutes. The available data show these effects, with the average value exceeding 21 × 10^6 j m^{-2} d^{-1} in many months; this value corresponds to 500 cal cm^{-2} d^{-1}, a typical maximum total at mid-latitudes. Nevertheless, during disturbances the flux can be reduced for periods of several days, and the value can drop below $^1/_{10}$ of this figure for a day or two at a time.

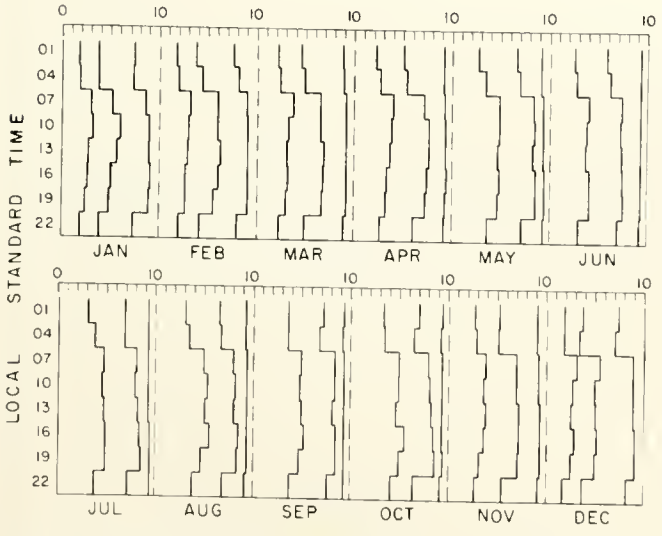

Fig. 3 Cloud cover data for Enewetak. For each month the three measures are the fraction of the sky obscured, in tenths, at least 75% (left), 50%, and 25% (right) of the time for each three hour period of the day.

Surface Wind

The surface wind data are shown in Fig. 4 as wind roses for each month (a) and for the entire year (b). As indicated in the key in Fig. 4b, in each rose the bar indicates the frequency of winds coming from that direction for each range of speed above calm. The numerical values beside each bar are the frequency, in percent, for wind from that direction and for that range of speed. The frequency of calms, to which no direction is assigned, is shown in the center of the circle. The frequency of occurrence of wind in each range of speed for all directions is shown, in percent, in the line below each rose. The wind

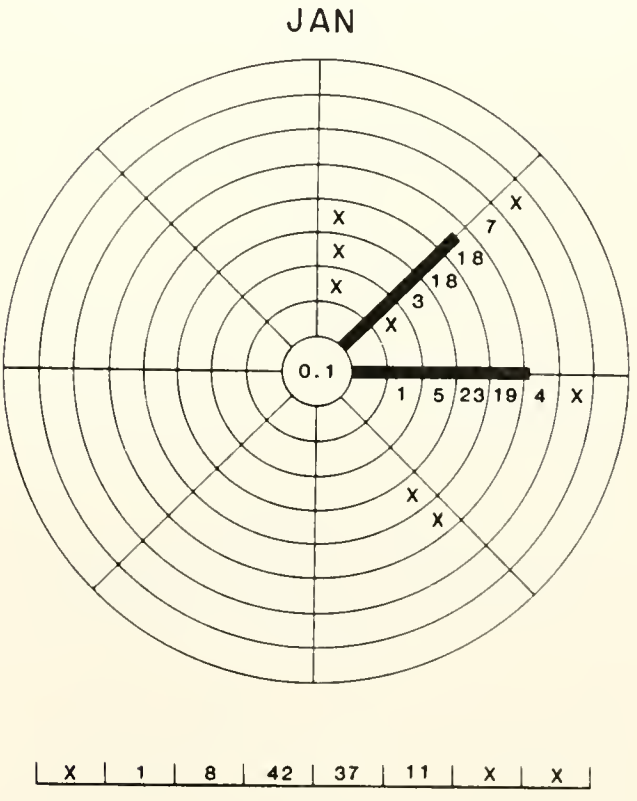

Fig. 4 Surface wind data for Enewetak. Wind roses for each month (a) and for the year (b). Frequency of wind for each directon and range of speed is shown by the printed figure beside the bar, which shows the frequency of winds for that direction for all speeds above calm. Frequency of calms is shown in the center of the circle. Frequency of wind speeds for all directions shown below each rose.

(Fig. 4a cont'd on next page)

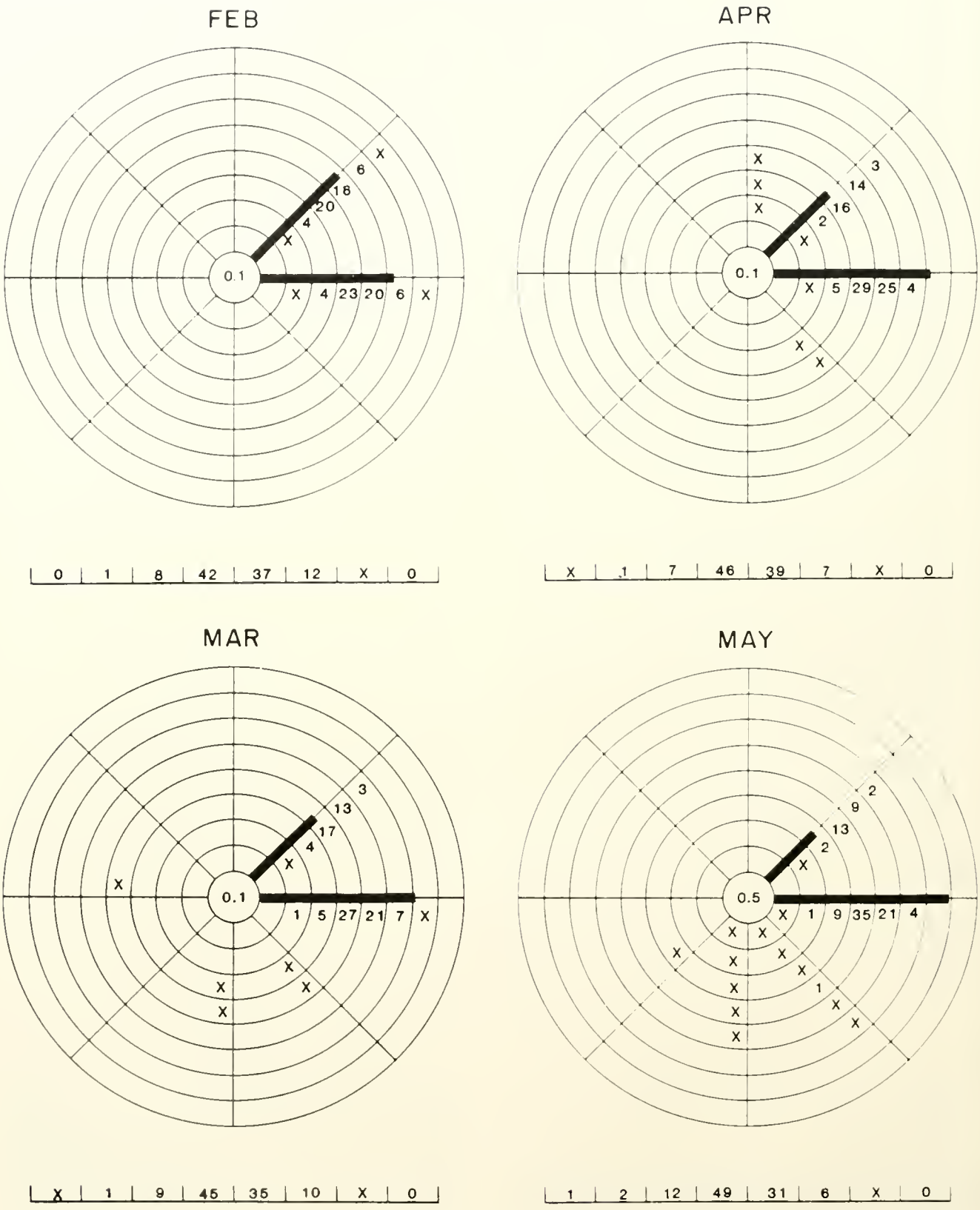

Fig. 4a cont'd.

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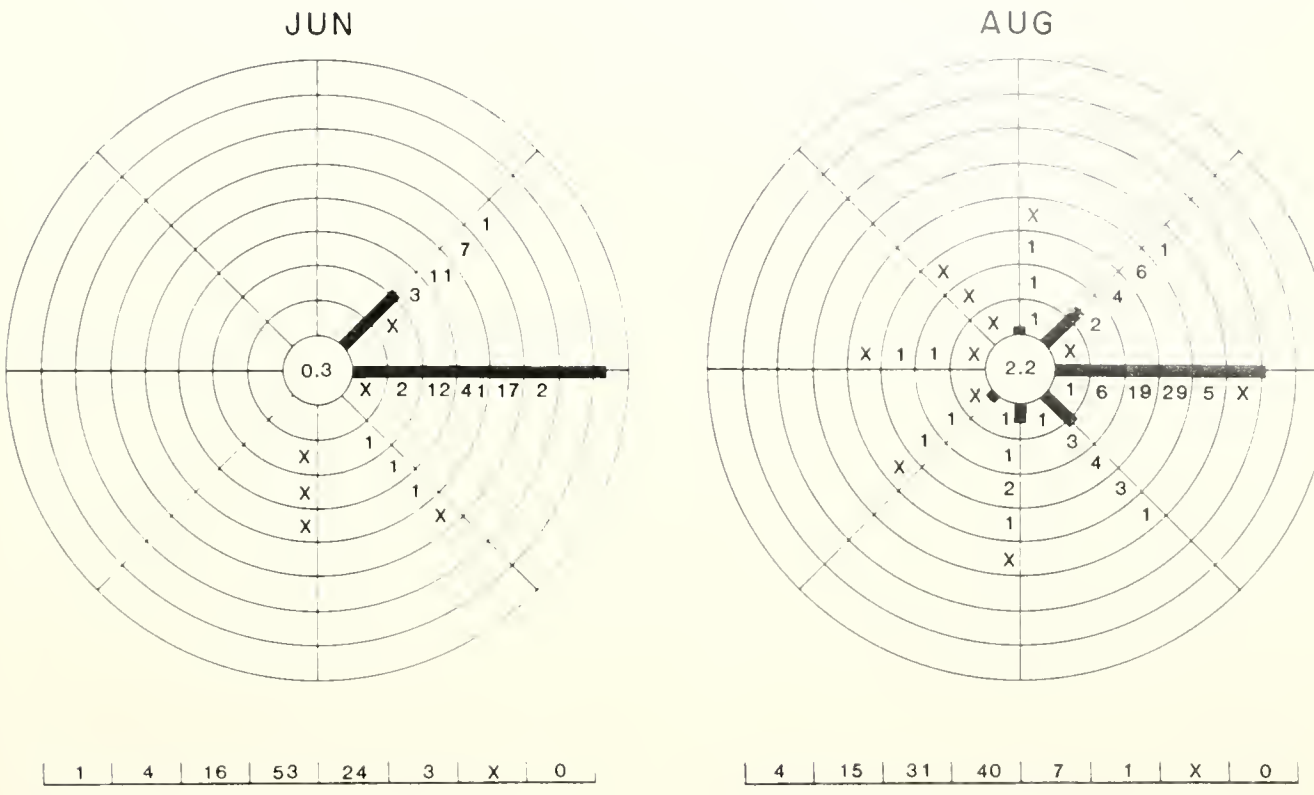

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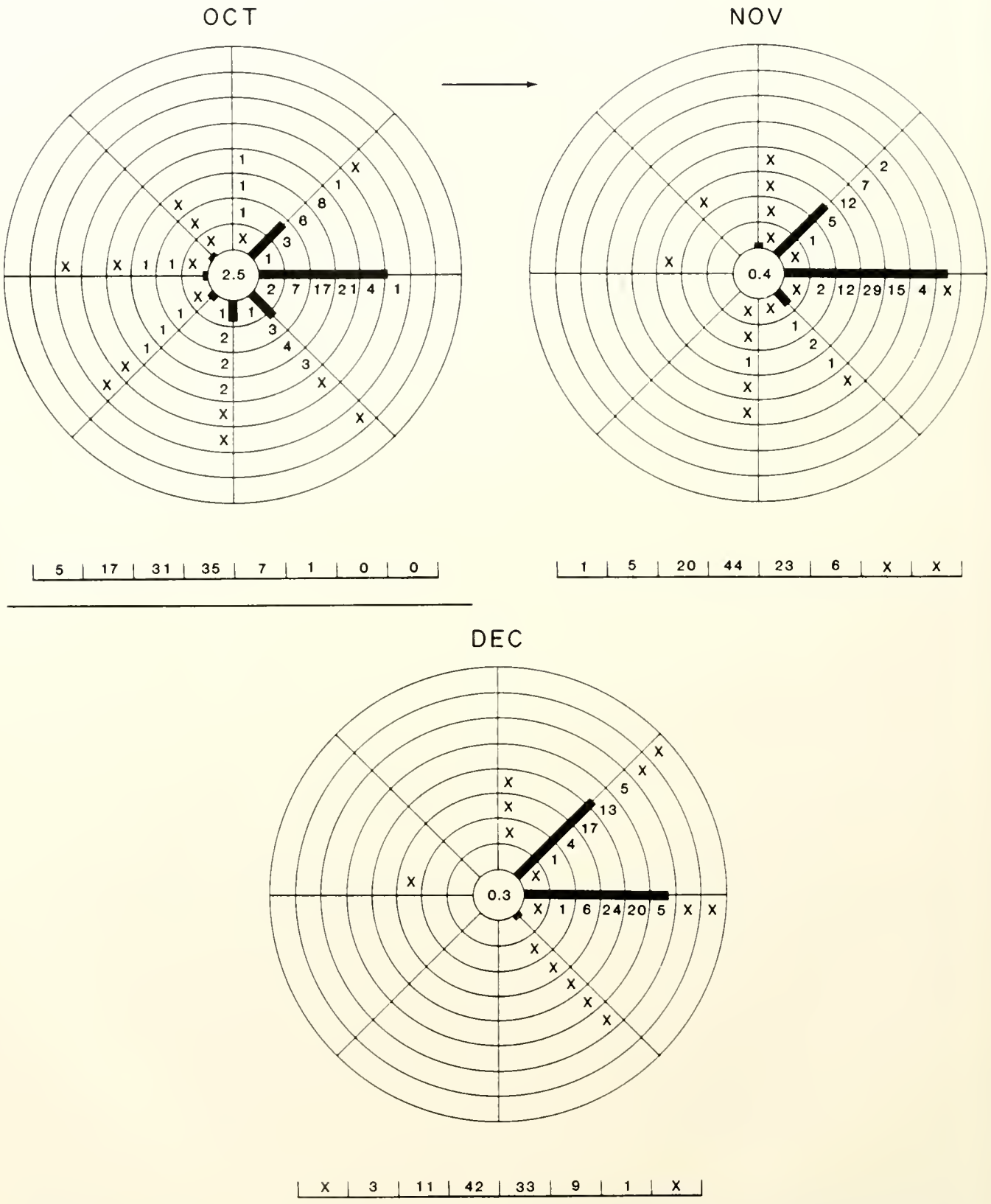

Fig. 4a cont'd.

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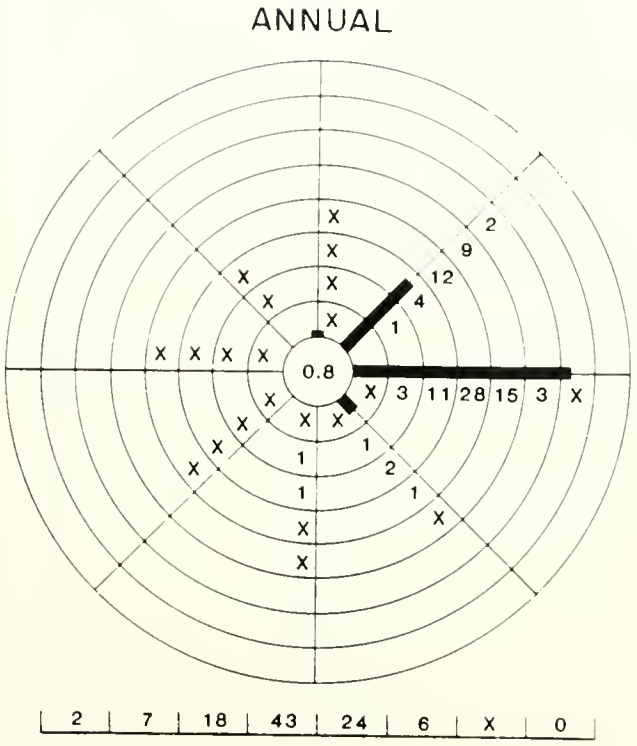
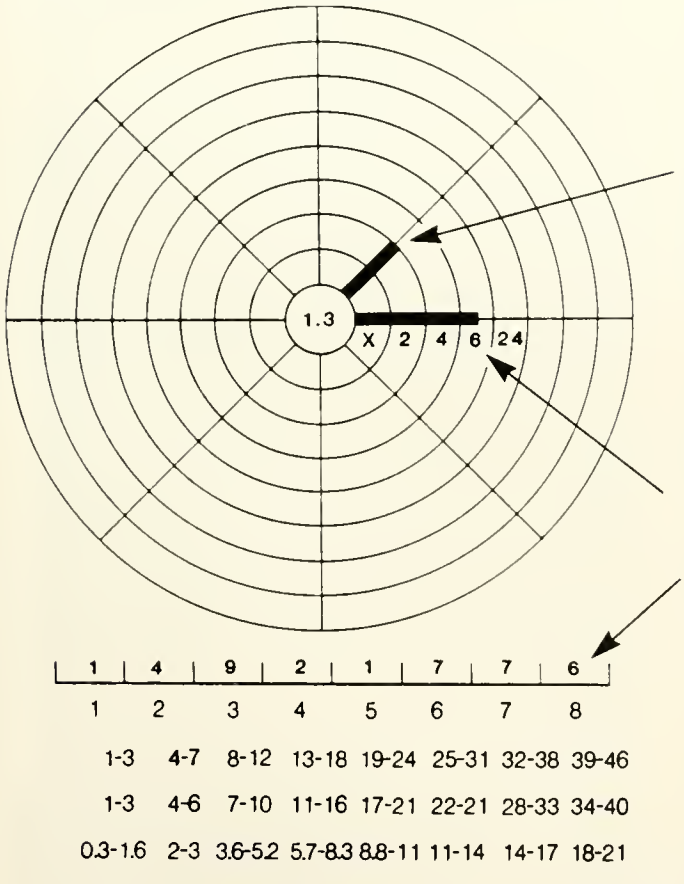


speed increments are indicated in the figure and are the traditional Beaufort scale values. The data are from U. S. Air Force records, as are the temperature and humidity data above, and were collected at various intervals, hourly over most of the period, with the instrument mounted at a height of 40 feet above sea level. The data are from the years 1945 to 1969 and again correspond in number to 14.1 years of continuous hourly observation. Thus the representativeness of these figures is good and falls in the range that one would expect from a sample of 10 to 20 years of continuous measurement. We have smoothed the data to report them at eight compass points but were careful to use a weighted averaging that preserves the rapid falloff of wind occurrence away from the predominant east and northeast directions.

This much-noted constancy of the wind is the first aspect of the rose data that we examine. During much of the year, the wind is from the northeast or east 95% or more of the time. From July through October, however, the peak broadens somewhat and moves a bit toward the south so that less than 20% of the winds are out of the northeast. The maximum frequency of winds from the less common directions (southeast around to north) is in August, September, and October, when disturbances are most common and when the equatorial trough is closest on



FREQUENCY OF CALMS: PERCENTAGE IS SHOWN IN CENTER OF CIRCLE.

DIRECTION FREQUENCY: BARS SHOW PERCENTAGE FROM EACH DIRECTION. EACH CIRCLE EQUALS 10%. 20% OF ALL WINDS FROM NE.

SPEED FREQUENCY: FIGURES SHOW PERCENTAGE FROM EACH DIRECTION IN EACH SPEED RANGE. 6% OF WINDS WERE FROM BETWEEN 13 AND 18 mph.

TABLE: FREQUENCY OF WIND FROM ALL DIRECTIONS FOR EACH SPEED RANGE.

SPEEDS ARE THE BEAUFORT SCALE:

MILES / HOUR

NAUTICAL MILES / HOUR

METERS / SEC

Fig. 4b

the average. The highest frequency of brisk winds is in the dry season, with over 45% of the hours having winds >8.5 ms^{-1} (19 mi h^{-1}). During the wet season the wind weakens substantially, particularly during August through October when >50% of the hours have wind <5.4 ms^{-1} (12 mi h^{-1}). Only during July through October are calms at all common, i.e., greater than 1% occurrence.

The dry season months exhibit the greatest constancy of pattern: >50% from the east and >40% from the northeast, with >75% frequency of speeds between 5.8 ms^{-1} and 10.7 ms^{-1} (13 and 24 mi h^{-1}). April does not differ much, except that the strength of the wind decreases slightly. In May and June the winds are strong out of the east, while in July through October the speed decreases and the direction varies more. In November the wind begins to shift back to the dry season pattern.

As these are average winds, the pattern of variation with time is lost. There is a consistent shift in the wind associated with easterly waves, the most common disturbance type in the wet season. The correlation of wind shifts with cloudiness and rainfall, obvious to anyone present during such events, is lost.

The annual average wind rose shown in Fig. 4 is easily understood given the monthly distributions discussed previously. Note that ⅔ of the time the wind is from 5.8 to 10.4 m/s (13 to 24 mi h^{-1}), and over 60% of the time the wind is from the east. Nevertheless, the annual average shows at least 0.1% winds from every direction.

Tropical Storms and Disturbances

While tropical storms strike the Marshall Islands infrequently, disturbances in the weather are a common and, on occasion, regular occurrence. Tropical storms of the greatest strength are called typhoons in the western Pacific, and they are, of course, extremely dangerous and destructive, particularly to exposed areas at low elevation such as Enewetak Atoll. Such storms grow from and are in fact the most fully developed form of tropical disturbance. We discuss the disturbances first because they are more numerous.

Several types of tropical disturbances are recognized in the literature; nevertheless, it is often impossible to classify a given weather system as one of the several types, even given estimates of the thermal structure and the movement and growth of the system. We are concerned primarily with the surface manifestation, so we shall only summarize what is known about the most common disturbance types.

During the wet season, particularly July through September, westward propagating wave-like systems are common in the tropics and have been observed and analyzed in the western Pacific and in the Caribbean and North Atlantic Ocean areas. In the western Pacific these easterly waves, on average, have a horizontal scale of 3500 to 4000 km and travel toward the west an average of 7° longitude per day (i.e., a mean velocity of 9 ms^{-1} or 20 mi h^{-1}); thus the disturbance affects a station for 4.5 to 5 days. During the passage of such a wave, there is a more or less systematic variation in the wind, cloud cover, and rainfall. The north–south component of the wind shifts, with maximum winds from the south of 1 to 2 ms^{-1} (2 to 5 mi h^{-1}) leading and maximum winds from the north following the center of the disturbance. The maximum cloudiness and rainfall occur just after the passage of the center of the disturbance. There is a temperature fluctuation, but it is hardly discernable at the surface. These waves can be observed with satellite images and are now understood to be an inherent property of deep easterly flow. The structure and detailed dynamic characteristics of such waves in the Marshall Islands area were studied by Reed and Recker (1971) using radiosonde and satellite data. The waves are most common in the wet season because the upper level winds are most favorable for their growth then. About ⅓ of such waves increase in intensity sufficiently to become classified as depressions or storms, but this occurs most commonly well west of the Marshall Islands.

Other types of disturbances are more uniformly distributed through the year but are even less easily classified. One type, the upper level cold-core low, is similar to the subtropical cyclone that is often observed in the Hawaiian area. In the Marshall Islands area, it may have no surface manifestation or may be accompanied by a weak but long-lived period of disturbed weather. In addition, there are squall lines and other short duration events which may produce strong winds and intense rainfall over limited areas as they pass.

Although both the frequency and the destructive power of tropical storms are greater in the far western Pacific than in the Marshall Islands area, such storms can threaten any tropical location. A sense of the seasonal distribution and the range of impact possible can be obtained from Table 2, which summarizes the depressions and storms that affected Enewetak between 1959 and 1979. Of course, the highest overall probability of tropical storm formation in the area is during the wet season, particularly July to October. However, there have been strong storms well within the dry season (e.g., Alice in 1979). The high winds and waves that extend to the periphery of such storms can have devastating consequences. There is a substantial body of literature on the effects of such storms on atolls, but the closest atoll so studied is Jaluit (Blumenstock, 1961). Specific data about individual storms are often sketchy, and prior to the operational use of satellite images, the tracking of past storms when far from land or shipping lanes may have been substantially in error. Nevertheless, there are useful data on several storms over the years, as indicated in Table 2.

Winds Aloft

The structure of the wind field above Enewetak Atoll is complex and variable. At time scales longer than 2 years, there are nearly periodic fluctuations at some levels, while at other levels there are short-period variations as important as those in mid-latitudes. In the following discussion,

TABLE 2

Tropical Storms and Disturbances Affecting Enewetak, 1959–1979

Year	Name, dates (GMT)	Remarks
1979	Alice, Jan. 5-6	Passed Kwajalein Jan. 3, was of typhoon strength at Enewetak. CD,* p. 91.
1976	Nancy, April 24-25	Strengthened from a depression to storm status as it crossed Enewetak; later became a typhoon. CD,* p. 102.
1976	Therese, July 7-8	Passed from SE to SW as a disturbance; later became a minimal typhoon. CD,* p. 100.
1972	Kathy, Oct. 28	Tropical depression at Enewetak, later a storm. CD,* p. 101.
1972	Olga, Oct. 24	Tropical storm at Enewetak, strengthened later to typhoon intensity. CD,* p. 100.
1971	Faye, Oct. 3	Disturbance and depression at Enewetak, later a tropical storm. CD,* p. 778.
1969	Phyllis, Jan. 18	Tropical storm. CD,* p. 78.
1967	Harriet, Nov. 17	Depression 100 miles south, later a typhoon. CD,* p. 76.

*CD, *Climatological Data*, National Summary, a NOAA publication from the Environmental Data Service, National Climatic Center, Asheville, N. C.

we emphasize the most important aspects of the upper level wind structure, proceeding upward from the surface and covering each 3-month period and the east–west and north–south components of the wind. The discussion is based on radiosonde data compiled and analyzed by Newell et al. (1972) and, to a lesser extent, on the illustration (their Fig. 4) of Blumenstock and Rex (1960).

The near-surface trade winds are strongest in the dry season, and they extend at least some 5 km or so into the atmosphere all the year around. The east–west component of the wind is negative, i.e., the wind is from the east, up to 500 mbar (~5.6 km) in March to May, and up to about 300 mbar (~9.5 km) in September to November. The westerly winds which overlie this layer are absent, in the long-term average, in December to February. The north–south component is near zero up to above 700 mbar (~3.0 km), with the average value being negative (i.e., from the north) in December to May and just positive (from the south) in June to November. This is consistent with surface wind roses presented above.

In the layer between 500 mbar (March to May) or 300 mbar (September to November) and ~150 mbar (14.5 km), there are westerly winds on the average in March to November and weak easterlies in the remainder of the year. The strongest westerly winds are in the months of March to May, centered in height around 200 mbar (~12.2 km). These are part of the subtropical jet which is strongest at higher latitudes and earlier in the year. The north–south component in this layer is, again, quite weak on the average. Due to the passage of large-scale weather systems, these mean winds are not representative of the observed circulation on a given day. Also, the weak north–south component is particularly sensitive to such variability, and this is all the more unfortunate as knowledge of this component is fundamental to understanding the large-scale transport, e.g., of heat and of tracers. While there are enough upper-air stations in the western tropical Pacific to make certain our knowledge of this component, there are vast areas in the mid-latitude Pacific where this is not so.

There is a quasi-biennial oscillation in the tropical stratosphere, i.e., the monthly averaged winds shift from west to east with a period of approximately 26 months in a band ~25° latitude wide (full width at half maximum amplitude) around the equator; this extends from very high in the stratosphere (>35 km) to at least 100 mbar (~16 km). This is now understood to be an interaction phenomenon illustrating the coupling between the troposphere and tropical stratosphere. Its discovery in the early 1960s illustrates how recently we have begun to learn about this area of the atmosphere. The "Krakatoa Easterlies," so named because they were first observed transporting debris from the spectacular 1883 volcanic eruption, are not as constant as had been thought.

Sources of Additional Data

Several of the important sources of additional meteorological data for Enewetak have been referenced in the previous sections. Here we summarize briefly the availability of various types of data and indicate the best sources for discussions on specialized subjects.

The archive of data used to prepare the figures in this chapter is the *Revised Uniform Summary of Surface Weather Observations for Eniwetok Marshall Islands*. In addition to the wind, cloudiness, temperature, and humidity data presented here, it contains extensive information important primarily for aircraft operations, e.g., ceiling and visibility data. The document can be obtained for copying costs from the National Climatic Center, Asheville, North Carolina.

A reliable and useful atlas of tropical wind and temperature charts is included in Newell et al. (1972) along with sophisticated discussions of the global tropical circulation in dynamical terms. The Pacific island rainfall data and analysis of Taylor (1973) are an excellent resource. There is a collection of marine meteorological observations (*Summary of Synoptic Meteorological Observations*, Volume 3, which includes "Area 10—Eniwetok") available from the National Technical Information Service as AD-725 138, but the data are very sparse.

Solar radiation data are available for certain periods beginning in May 1977 from the Department of Meteorol-

ogy, University of Hawaii. They are tabulated as hourly totals of the shortwave radiant energy flux, in cal cm^{-2} h^{-1}. Because the data coverage is not continuous (no period longer than 8 months is available without extended interruption), it is not presented here.

Many useful and interesting data were collected by Blumenstock and Rex (1960) in addition to those discussed previously.

ATMOSPHERIC CHEMISTRY OF ENEWETAK ATOLL

Introduction

During the period April to August 1979, an extensive program investigating the chemistry of atmospheric trace gases, particles, precipitation, and dry deposition was undertaken at Enewetak Atoll. The Sea/Air Exchange Program, or SEAREX, was sponsored by the National Science Foundation and involved efforts by 11 institutions from the United States, France, and Great Britain. The impetus for this atmospheric chemistry study was the increasing interest in the possibility that significant quantities of both natural and anthropogenic substances may be transported to the ocean via the atmosphere in mid-ocean regions. An understanding of the importance of the atmosphere as a transport path is critical in determining the basic geochemical cycles and budgets of a variety of naturally occurring substances and in predicting the near-global impact of anthropogenic material in open ocean regions. The objectives of the study were to investigate the concentrations and sources of selected inorganic and organic substances in the marine atmosphere at Enewetak, their flux into the ocean, and the mechanisms of their exchange with the ocean. Substances investigated included trace metals such as lead, cadmium, zinc, selenium, copper, iron, antimony, manganese, mercury, silver, aluminum, and the alkali and alkaline earth metals; soil dust; atmospheric sea salt; ^{210}Pb and its daughter ^{210}Po; particulate organic carbon; and organic compounds such as PCBs, DDT, aliphatic hydrocarbons, phthalate plasticizers, fatty acids, fatty and polycyclic alcohols, and low molecular weight ketones and aldehydes.

The atmospheric chemistry studies at Enewetak Atoll took place on Bokandretok Island, just north of Enewetak Island (Fig. 5). During late November and December 1978, an 18-meter-high walk-up sampling tower and three small buildings were constructed on Bokandretok. The sampling tower, located directly on the east coast of the island, was necessary to get above any local contamination from both man-made sources and natural sources such as erosion products and surf spray generated when waves strike the shoreline.

Additional precautions were taken against local contamination. Sampling pumps were located on the ground and were connected to the collection systems on top of the tower by 20 meters of hose. The operation of the pumps

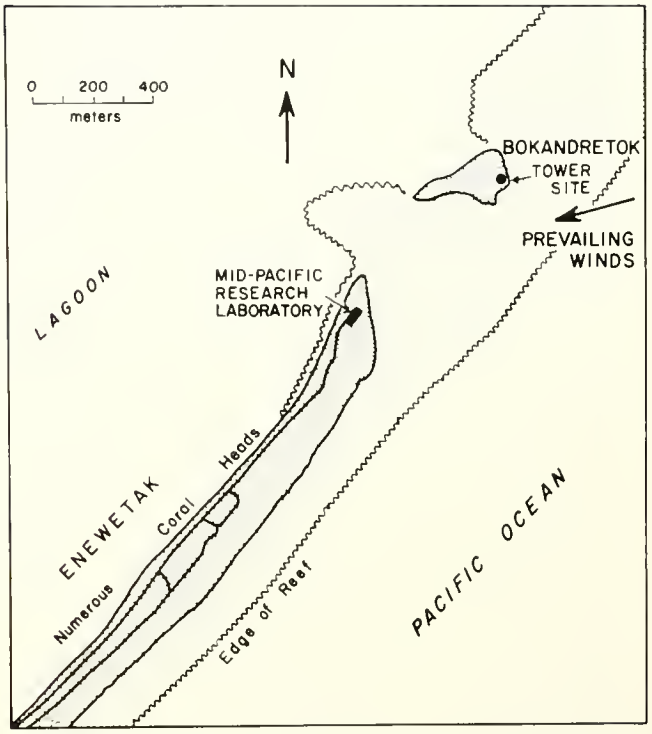


Fig. 5 SEAREX tower site on Bokandretok Island, just northeast of the Mid-Pacific Research Laboratory on Enewetak.

was controlled automatically as a function of local wind speed, direction, and total condensation nuclei in the ambient air. Pumps were shut down when the wind direction could cause local contamination from Bokandretok or other islands in the atoll, when the speed was less than 2.5 ms^{-1}, or when the condensation nucleus count was greater than 300 to 400 cm^{-3}, a typical background level for marine air. The air sampling tower on Bokandretok is shown in Fig. 6.

The SEAREX experiments were scheduled to begin in early January 1979. However, on Jan. 5, 1979, Typhoon Alice struck Enewetak with winds over 50 ms^{-1} and very high tides. The SEAREX tower and one building on Bokandretok survived but with some damage. The remaining buildings and the submarine cable supplying power to Bokandretok were destroyed. The experiments were delayed until repairs could be made, and sampling began in April 1979.

Atmospheric Sea Salt

The ocean is the largest source for particles, on a mass basis, in the global atmosphere. These sea salt particles are produced when wave-produced bubbles burst at the ocean surface (Woodcock, 1953; Blanchard, 1963). Concentrations of this sea salt are extremely high immediately downwind of surf breaking on a reef or a shoreline. In these areas, atmospheric sea salt concentrations can easily

Fig. 6 SEAREX atmospheric sampling tower in operation on Bokandretok Island in 1979.

approach 1 mg m^{-3} up to several meters downwind from the surf line (Duce and Woodcock, 1971). Samples of atmospheric salt collected from the top of the tower at Enewetak were not affected by the surf zone, as the high concentrations produced on the shoreline were carried beneath the top of the tower by the strong trade winds. Thus the atmospheric salt concentrations measured on the tower were representative of concentrations expected over the open ocean at that elevation (18 m) above the sea surface.

Measured 18-meter-high salt concentration at Enewetak ranged from about 15 $\mu g\ m^{-3}$ at winds of 5 to 6 ms^{-1} to about 30 $\mu g\ m^{-3}$ at winds of 10 ms^{-1} (McDonald et al., 1982). The higher winds result in more wave and whitecap activity and thus higher atmospheric salt concentrations.

The mass median radius of the sea salt collected on the tower was 3 to 4 μm at the mean observed relative humidity of 80%, and generally 90% or more of the salt was present on particles with radii greater than 1 μm. McDonald et al. (1982) showed that the rate of deposition

of the salt to the island surface was also very wind speed dependent but increased with wind speed much more rapidly than the sea salt concentration itself (Table 3).

TABLE 3

Atmospheric Sea Salt Concentrations and Deposition at Enewetak*

Wind speed, ms^{-1}	Atmospheric salt concentration, $\mu g\ m^{-3}$	Atmospheric salt deposition, $ng\ cm^{-2}\ h^{-1}$
3.4†	3	8
6.5	16	170
10	29	410

*Measured 18 m above sea level (McDonald et al., 1982).

†3.4 ms^{-1} data obtained from Pigeon Key, Florida.

These authors pointed out that this is because larger salt particles are present in the atmosphere at higher wind speeds, and these larger particles have a much higher deposition, or settling, velocity than the smaller particles. With their much shorter atmospheric residence times, a relatively low concentration of larger particles can dominate the flux of the entire particle population. For example, at a wind speed of 2.4 ms^{-1}, particles with a radius (at 80% relative humidity) of 4.5 μm or smaller account for 60% of the total salt mass but less than 10% of the salt deposition, while salt particles with radii greater than 10 μm account for only 13% of the salt mass but 70% of the deposition.

Asian Soil Dust

The geographical distribution of some mineral components, such as quartz and illite, in North Pacific marine sediments suggests that the atmosphere may be a very important transport path for mineral matter, or soil dust, to mid-latitude (30° to 40°N) areas of the North Pacific. There are, however, few data available on the dust concentration in the atmosphere over the North Pacific and no direct information on the atmospheric input rate of this material to the ocean surface. During the SEAREX experiments, air filter samples were collected for dust analysis. The atmospheric concentration of aluminum was used as an indicator of continental dust in these samples, with the dust containing about 6.5% Al in the aluminosilicate matrix. The observed concentrations of dust and salt in the atmosphere at Enewetak are shown in Fig. 7. While the atmospheric salt concentration remained relatively constant, the dust concentration dropped by a factor of ~100 from mid-April to early August 1979 (Duce et al., 1980).

The high concentrations of soil dust observed at Enewetak were unexpected, especially since Enewetak lies well within the easterly tradewind regime, and the nearest

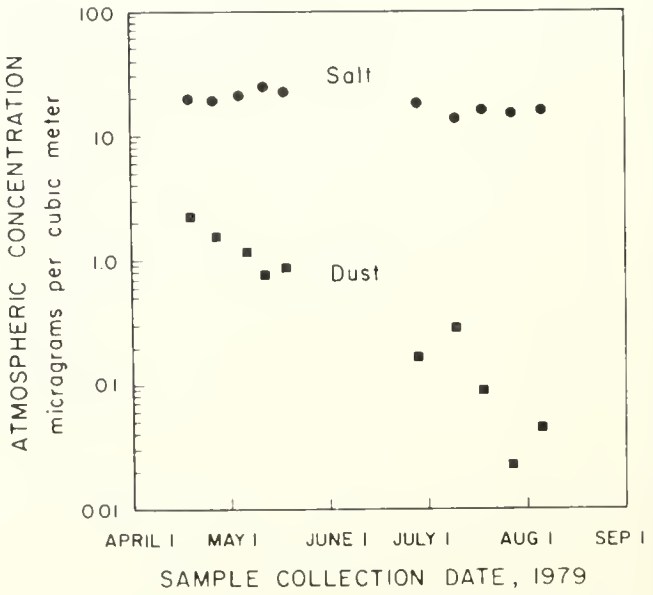


Fig. 7 Atmospheric concentrations of dust and sea salt at Enewetak between April and August, 1979.

continental land mass, Asia, is about 5000 km to the northwest. The dramatic decrease in dust over the 5-month period was also unexpected, but both these observations can be explained on the basis of the seasonal changes in the large-scale wind patterns over the North Pacific and the seasonal character of dust storm activity in the Takla Makan, Gobi, and Ordos Desert regions of China. Dust storm activity is apparently greatest in the spring in China due to the combined effects of low rainfall, the increased occurrence of high surface winds associated with strong cold fronts, and soil freshly plowed for planting. The mean surface winds from March through May are strong easterlies over the western North Pacific between 30°N and the equator; north of 30°N, the surface winds are weak, with a tendency toward being westerly. However, at 700 mbar (about 3000 m) there is very strong westerly flow north of about 20°N extending from well within Asia to the central North Pacific. Thus dust raised over China could easily be transported by the mean winds at this level to the region north of Enewetak. During June through August, however, conditions are not favorable for the transport of dust to the central North Pacific. Surface winds are easterly from Enewetak northward to about 40°N. At 700 mbar the northern boundary of the easterlies is located at about 30°N. Persistent westerlies appear at 700 mbar only north of 40°N, and they are very weak. Thus we would generally expect much higher atmospheric soil dust concentrations and deposition rates to the ocean at Enewetak in the late winter and spring than the rest of the year. In corroboration of this, Ing (1972) documented an April 1969 dust storm over China, and satellite photos showed that dust cloud moving well out over the East China Sea.

The observed mass median radii for the Asian dust in the SEAREX study at Enewetak ranged from 0.7 to 1.0 μm, considerably smaller than the atmospheric salt particles. Eighty to 85% of the mass of the dust was present on particles with radii between 0.2 and 2 μm. This is consistent with a very long atmospheric transport path.

Removal of dust to the ocean by rain and dry deposition was estimated at Enewetak through the analysis of rain samples and samples obtained by the exposure of flat plates on top of the tower. The total (wet and dry) deposition of dust during May 1979 was estimated as about 4 $\mu g\ cm^{-2}$. Assuming this deposition was applicable for 3 to 5 months during the spring and early summer, with somewhat lower deposition the rest of the year, leads to an estimated annual atmospheric dust deposition to the ocean near Enewetak of 15 to 30 $\mu g\ cm^{-2}$ (Duce et al., 1980). Settle and Patterson (1982) report dust in rain and dry deposition at Enewetak which converts to a yearly flux of about 13 and 1 $\mu g\ cm^{-2}$ respectively, the latter being recycled in sea spray and not contributing to net input. These inputs can be compared with an estimate of the annual nonbiological marine sedimentation rate to the ocean floor in that region of about 50 $\mu g\ cm^{-2}$ (M. Leinen, personal communication). Within the uncertainties in both estimates, it is clear that the atmosphere is a significant transport path for the nonbiological material found in marine sediments near Enewetak. It is also clear that the transport of Asian derived substances to the Enewetak region is seasonal.

Lead-210 was also measured in the atmosphere at Enewetak. Lead-210 is a radioactive nuclide produced in the atmosphere by the decay of gaseous ^{222}Rn, which in turn is derived from continental soils. Atmospheric ^{210}Pb was found to decrease over the April to August 1979 period in a manner similar to the atmospheric Al concentration. Lead-210 in air ranged from about 4 dpm per 1000 m^3 in April to 0.8 to 1.0 dpm per 1000 m^3 in late July and August (Turekian and Cochran, 1981a, b). Using ^{210}Pb as an indicator of Asian dust transport, Turekian and Cochran (1981a, b) calculated a dust deposition of about 10 $\mu g\ cm^{-2}\ yr^{-1}$ to the ocean at Enewetak.

Trace Metals

A number of trace metals were investigated on particles in the atmosphere at Enewetak. Some of these trace metals, e.g., Na, Mg, K, and Ca, were clearly derived from the ocean as part of the atmospheric sea salt. Interelemental concentration ratios among this group were the same as found in seawater. Another group of metals was clearly associated with the mineral aerosol or Asian dust. This was determined by using the Al content of the particles as a reference element for crustal weathering products and comparing the metal/Al ratio on the aerosols to the average metal/Al ratio in the earth's crust. An enrichment factor relative to the crust, EF_{crust}, can be defined as follows:

$$EF_{crust} = \frac{(X/Al)_{air}}{(X/Al)_{crust}}$$

where $(X/Al)_{air}$ and $(X/Al)_{crust}$ refer to the mass ratio of metal X to aluminum in the Enewetak aerosols and the earth's crust, respectively. Values of EF_{crust} near 1 for any metal suggests that crustal weathering is likely its source in the particles (Duce et al., 1975; Rahn, 1976). EF_{crust} values for samples collected at Enewetak are given in Table 4. From this table it is clear that such elements as Al, Ta, Sc, Mn, Fe, Eu, Ni, Co, V, Hf, Cr, Th, Cu, and Rb are primarily found associated with mineral or soil aerosol particles at Enewetak. Metals with an EF_{crust} value higher than 4, e.g., Zn, Cs, Sb, Ag, Pb, Cd, and Se, apparently have some source other than continental weathering.

TABLE 4

Geometric Mean EF_{crust} Values for Atmospheric Trace Metals at Enewetak*

Metal	EF_{crust}	Metal	EF_{crust}
Ta	0.7 ± 1.1†	Cr	1.8 ± 1.2
Sc	0.8 ± 1.1	Th	2.0 ± 1.1
Mn	0.9 ± 1.1	Cu	2.3 ± 1.6
Al	1.0	Rb	3.0 ± 1.2
Fe	1.0 ± 1.1	Zn	4.6 ± 1.1
Eu	1.0 ± 1.1	Cs	4.8 ± 1.1
Ni	1.0 ± 1.1	Sb	27 ± 1.3
Co	1.0 ± 1.1	Ag	44 ± 1.8
V	1.6 ± 1.6	Pb	45 ± 2.9
Hf	1.6 ± 1.1	Cd	57 ± 4.8
		Se	3000 ± 1.9

*From Duce et al., 1981.
†Geometric standard deviation.

On the basis of the measurements made at Enewetak in 1979, Table 5 presents the expected mean atmospheric concentrations for a number of trace metals during the March to June (high Asian dust) period and during the rest of the year (Duce et al., 1981). Concentration units are ng (10^{-9} g) and pg (10^{-12} g) per cubic meter of air. Note that the concentration of all the metals is higher in the spring than the rest of the year, although the increase in concentration for many metals during the spring is not as great as for the metals clearly associated with the dust. For example, while the mean dust associated metals are ~25 times higher in the spring, the difference for Pb is less than a factor of 2, Se is about 2, Cd is 5, etc. We assume the source of these "enriched" metals is also primarily continental regions. Metals associated primarily with the desert dust have considerably higher concentrations during the spring and early summer due to both stronger source functions (i.e., more frequent dust storms) and wind fields which are conducive to effective long-range transport to Enewetak during that period. However, the enriched elements may have continental sources which are not so seasonal in nature but which are

TABLE 5

Mean Atmospheric Concentrations of Trace Metals at Enewetak*

	March–June, ng m^{-3}	Rest of year, ng m^{-3}
Al	75	3
Fe	50	2
Mn	1	0.04
Ba†	1	0.02
	pg m^{-3}	pg m^{-3}
Sc	20	1
Cr	200	30
Co	25	1
Eu	2	0.1
Cs	15	0.5
Hf	5	0.2
Rb	200 (5500†)	40 (60†)
Ta	1.5	0.1
Th	20	1
V	120	20
Zn	250	80
Cd	10	2
Cu	50	10
Pb	150(230†)	100(120†)
Se	200	100
Sb	5	1
Ag	5	< 1

*From Duce et al., 1981, except as noted.

†From Settle and Patterson, 1982.

TABLE 6

Estimates of Annual Atmospheric Deposition of Trace Metals to the Ocean at Enewetak*

	Atmospheric deposition			Marine sedimentation
	Wet	Dry	Total	
Al, μg cm^{-2}	1.5	0.4	1.9	3.3
Fe, μg cm^{-2}	1.0	0.3	1.3	2.0
V, ng cm^{-2}	3	4	7	5†
Sc, ng cm^{-2}	0.3	0.08	0.4	0.9†
Cr, ng cm^{-2}	5	1†	6	2†
Eu, ng cm^{-2}	0.04	0.006†	0.05	0.05†
Cs, ng cm^{-2}	0.3	0.08†	0.4	0.2†
Th, ng cm^{-2}	0.7	0.2†	0.9	0.4†
Ta, ng cm^{-2}	0.03	0.008	0.04	0.08†
Hf, ng cm^{-2}	0.1	0.03	0.13	0.1†
Rb, ng cm^{-2}	6	1.6	8	4†
Cu, ng cm^{-2}	2	6	8	7
Mn, ng cm^{-2}	13	5	18	250
Co, ng cm^{-2}	0.5	0.1†	0.6	2
Pb, ng cm^{-2}	8(6‡)	~4(6‡)	~12(12‡)	0.6¶§
Zn, ng cm^{-2}	15	~7	~22	7
Cd, ng cm^{-2}	0.6	<0.8	~1	0.02¶
Se, ng cm^{-2}	5	5**	10	0.007¶
Sb, ng cm^{-2}	0.12	0.12**	0.24	0.02¶
Ag, ng cm^{-2}	0.2	~0.5	~0.7	—

*From Duce et al., 1981.
†Estimated from Al.
‡From Settle and Patterson, 1982.
¶Estimated from average marine clay composition.
§Sum of 0.3 authigenic plus 0.3 silicate lattice.
**Estimated from Pb.

more uniformly distributed throughout the year. Thus their smaller change in concentration from spring to the rest of the year may largely reflect the changes in atmospheric circulation patterns for those time periods.

From measurement of these trace metals in rain and dry deposition, estimates can be made of their atmospheric deposition to the ocean surface at Enewetak (Duce et al., 1981). The temporal variation in atmospheric concentrations shown in Table 5, the monthly rainfall amounts at Enewetak (Fig. 2a), and the measured concentrations of these metals in rain and dry deposition were taken into consideration when the total deposition rates given in Table 6 were calculated. Note that the data in Table 6 suggest that both wet and dry deposition are important for all elements. There is evidence, however, that much of the measured dry deposition of at least some of these metals may be the result of metals being recycled from the sea surface on sea salt aerosols (Duce, 1982; Settle and Patterson, 1982). This would mean the dry deposition values do not represent a net input of these metals to the ocean. Thus the numbers presented in Table 6 probably represent an upper limit relative to net inputs from the atmosphere to the ocean.

Marine sedimentation rates for these metals are presented in Table 6 and have been determined from the chemical analysis of surface sediments collected near 29°N 159°W. An estimate of the overall sedimentation rate near Enewetak was determined from mapping measured sedimentation rates over the entire North Pacific (M. Leinen, personal communication). Where the surface sediments were not analyzed for a particular metal, crustal ratios to Al were used for elements present in crustal abundance in the atmosphere, and average marine clay composition was assumed for the atmospherically enriched elements.

It is apparent that the atmospheric deposition to the ocean and the marine deposition to the sediments are very close for Al, Fe, V, Sc, Cr, Eu, Cs, Th, Ta, Hf, Rb, and Cu, suggesting atmospheric transport is very important for marine sedimentation of these metals near Enewetak. Atmospheric input accounts for only a small part of the Mn and Co in the sediments. However, the atmospheric input of Pb, Zn, Cd, Se, and Sb to the ocean is apparently considerably greater than the deposition of these elements to the sediments. There are at least two possible explanations for these latter results. First, this would be expected if the atmospheric concentrations and deposition rates of

these metals had resulted from pollution sources on the continents, since the marine sedimentation rates for these metals are mean rates applicable to approximately the past 15,000 years. Input of pollution-derived trace metals, which has developed significantly only in the past 50 years or so, would not be reflected in the measured marine sedimentation rates. Schaule and Patterson (1982) proposed that a shift may have occurred from principally fluvial inputs of lead to the oceans in earlier times to primarily atmospheric input in recent times. Second, these results would also be expected if a significant fraction of the atmospheric deposition of these trace metals came from their recycling from the ocean surface into the atmosphere and back to the ocean. Recent studies (Weisel, 1981) suggest that recycling of marine-derived metals probably does not account for more than a few percent of the mass of these metals in the atmosphere at Enewetak. However, since these ocean-derived metals would be found on the large sea salt particles, their dry deposition back to the ocean surface could be rather high (Duce, 1982). Thus, while it is believed that most of the mass of the enriched trace metals in the atmosphere at Enewetak is derived from the continents and very possibly from pollution sources, a significant fraction of the gross dry deposition of these metals into the ocean from the atmosphere may be due to recycled metals from the ocean surface, as mentioned above.

Lead isotope ratios reported by Settle and Patterson (1982) confirm that, during the high dust period in April 1979, the pollution-derived Pb had an Asian origin (Tables 7a and b). However, as the Asian dust decreased, the $^{206}Pb/^{207}Pb$ ratio increased and became similar to that for pollution-derived Pb from North America. Thus some, if not most, of the small particle pollution-derived Pb found at Enewetak in the summer may have been transported from North America to Enewetak. On the basis of ^{210}Pb and stable lead measurements, Settle et al. (1982) and Settle and Patterson (1982) calculated a net atmospheric stable lead deposition rate of 4 to 10 ng cm^{-2} yr^{-1} at Enewetak. This agrees well with the value of 8 to 12 ng cm^{-2} yr^{-1} given in Table 6.

The mass median radii (MMR) for the particles containing the various trace metals are presented in Table 8. Note that the sea salt metals (Na, Mg, K, and Ca) have MMRs near 3.5 μm while the crustally derived metals have MMRs of 0.75 to 1.0 μm. The enriched metals (Zn, Se, Sb, and Pb) have MMRs of <0.5 μm, consistent with a possible pollution source for these elements.

TABLE 7a

$^{206}Pb/^{207}Pb$ Ratios in Filtered Air Sample at Enewetak*

Collection date, 1979	$^{206}Pb/^{207}Pb$
4/22 to 5/09	1.170
5/09 to 5/15	1.196
7/12 to 8/10	1.205

TABLE 7b

$^{206}Pb/^{207}Pb$ Expected from Major Continental Sources*

Region	$^{206}Pb/^{207}Pb$ ratio
Asia/Japan	1.153 to 1.165
U. S. A.	1.190 (1974) to 1.230 (1978)
Mexico	1.187

*From Settle and Patterson, 1982.

TABLE 8

Mean Particle Mass Median Radii (MMR) for Trace Metals at Enewetak*

Element	MMR, μm	Element	MMR, μm
Na	3.4	Hf	0.80
Mg	3.5	Rb	1.1
K	3.4	Th	0.84
Ca	3.5	Ta	0.74
Al	0.80	Co	0.75
Fe	0.72	Eu	0.88
Mn	0.88	Ce	0.81
V	0.76	Pb	0.25
Cu	0.96	Se	0.53
Sc	0.70	Sb	~0.35
Cs	0.79	Zn	0.04

*From Duce et al., 1981.

Gaseous and particulate mercury were also investigated at Enewetak (Fitzgerald et al., 1981). The concentrations observed are given in Table 9. It is apparent that mercury exists almost entirely as a gas at Enewetak. The relatively small temporal variation in gaseous Hg concentration (and the fact that similar concentrations are found at other marine areas) suggests a relatively long atmospheric

TABLE 9

Atmospheric Mercury at Enewetak*

Collection period, 1979	Gaseous Hg, ng m^{-3}	Particulate Hg, ng m^{-3}
4/27 to 5/21	1.6 ± 0.6	0.0005
6/28 to 8/6	1.7 ± 0.5	0.0012

*From Fitzgerald et al., 1981.

residence time for the vapor phase. Studies of Hg speciation in the atmosphere at Enewetak indicate that the gas phase is principally inorganic mercury, of which elemental Hg is probably the major component. Mercury in rain at Enewetak was found to have a concentration of 2 ng l^{-1}. Apparently this concentration is derived primarily from the washout of the particulate Hg rather than the vapor phase.

Organic Carbon

The organic carbon concentration of atmospheric particles at Enewetak was ~0.9 $\mu g\ m^{-3}$ (Chesselet et al., 1981) (Table 10). This is typical of marine regions, where the concentration generally ranges between 0.2 and 1.2 $\mu g\ m^{-3}$. Eighty to 85% of the mass of this organic carbon at Enewetak is found on particles with radii less than 1 μm.

TABLE 10

Atmospheric Organic Carbon at Enewetak

	Concentration		
	$\mu g\ m^{-3}$	$mg\ l^{-1}$	Reference
Particulate	0.89 ± 0.17		Chesselet et al., 1981
Rain		0.64 ± 0.48	Gagosian et al., 1981b

Carbon isotope studies by Chesselet et al. (1981) have suggested strongly that the small particle (<1 μm) organic carbon does not have a marine origin. By measuring both ^{12}C and ^{13}C, one can calculate $\delta^{13}C$ as follows:

$$\delta^{13}C = \left[\frac{(^{13}C/^{12}C)_{sample}}{(^{13}C/^{12}C)_{standard}} - 1 \right] \times 1000$$

$\delta^{13}C$ values calculated for the smallest particles ($r < 1\ \mu m$) are $-26°/_{oo}$ to $-28°/_{oo}$. Chesselet et al. (1981) point out that this range is similar to $\delta^{13}C$ values for continental vegetation, coal, and the products of petroleum combustion, $-26 \pm 2°/_{oo}$, suggesting the small particle carbon is of continental origin. The $\delta^{13}C$ values for the larger particles ($r > 1\mu m$) are $-18°/_{oo}$ to $-22°/_{oo}$. This is similar to the $\delta^{13}C$ value for marine organic carbon, which is generally $-21 \pm 2°/_{oo}$ in low latitude regions (40°S to 50°N), suggesting the large particle carbon in the Enewetak marine atmosphere is of marine origin.

The organic carbon content of rain at Enewetak averaged 1.2 mg l^{-1} during April and May and 0.3 mg l^{-1} during July and August 1979 (Gagosian et al., 1981b).

Organic Lipid Class Compounds

Particulate and vapor phase heavy n-alkanes were measured independently in the atmosphere at Enewetak by two research groups in 1979. The observed concentrations are reported in Table 11. It is apparent that the vapor phase dominates the concentration of these compounds, at least from n-C_{21} to n-C_{30}, and probably for the lower carbon number alkanes as well. Duce and Gagosian (1982) used the concentration distribution in Table 11 to model the input of particulate n-alkanes (n-C_{15} to n-C_{30}) and vapor phase n-alkanes (n-C_{10} to n-C_{30}) from the atmosphere to the ocean. Consideration was given to rain scavenging of both aerosol and vapor phase n-alkanes, dry deposition of aerosol n-alkanes, and direct gas exchange with the ocean of vapor phase n-alkanes. Estimates of the atmospheric input of n-alkanes to the ocean at Enewetak are given in Table 12. Note that rain scavenging of n-alkanes on particles appears to be the primary method of n-alkane removal from the atmosphere.

TABLE 11

Atmospheric N-Alkanes at Enewetak

	Concentration		
	Particulate,*	Gaseous	
N-alkane	$ng\ m^{-3}$	$ng\ m^{-3}$*	$ng\ m^{-3}$†
n-C_{13}			0.23
n-C_{14}			0.19
n-C_{15}			0.66
n-C_{16}			0.13
n-C_{17}			0.55
n-C_{18}			0.07
n-C_{19}			0.07
n-C_{20}			0.07
n-C_{21}	0.0017		0.07
n-C_{22}	0.0020		0.07
n-C_{23}	0.0023		0.09
n-C_{24}	0.0021		0.12
n-C_{25}	0.0030	0.095	0.12
n-C_{26}	0.0020	0.088	0.09
n-C_{27}	0.0067	0.055	0.07
n-C_{28}	0.0037	0.024	
n-C_{29}	0.0170	0.019	
n-C_{30}	0.0033	0.013	

*Gagosian et al., 1981b, 1982.

†Atlas and Giam, personal communication, 1981.

It can be seen from Table 11 that the odd carbon number n-alkanes on aerosols have higher concentrations than the adjacent even carbon number n-alkanes. This is observed for higher n-alkanes up to n-C_{36} as well (Gagosian et al., 1980). The odd-to-even carbon preference index and the fact that the major alkanes are n-C_{27}, n-C_{29}, and n-C_{31} strongly suggest that the source of these heavier n-alkanes present on aerosols is vascular plant waxes, probably of Asian origin (Gagosian et al., 1981a).

Concentrations of fatty alcohols, fatty acid esters, and fatty acid salts were also measured in the Enewetak atmosphere and are presented in Table 13 (Gagosian et al.,

TABLE 12

Estimate of Annual Atmospheric Deposition of n-C_{10} to n-C_{30} Alkanes to the Ocean at Enewetak*

Deposition mechanism	Deposition rate, 10^{-10} g cm^{-2} yr^{-1}
Particulate:	
Wet	6.2 to 62
Dry	0.8 to 8
Vapor Phase:	
Wet	0 to 0.00001
Dry	0 to 1.4
Total	7 to 71

*From Duce and Gagosian, 1982.

TABLE 13

Concentration of Fatty Alcohols, Fatty Acid Esters, and Fatty Acid Salts on Atmospheric Particles at Enewetak*

Organic substance	Concentration range, pg m^{-3}
Fatty alcohols	
C_{13}–C_{20}	2 to 85
C_{21}–C_{32}	58 to 210
Fatty acid esters	
C_{13}–C_{20}	34 to 290
C_{21}–C_{32}	6 to 91
Fatty acid salts	
C_{13}–C_{20}	87 to 4000
C_{21}–C_{32}	36 to 670

*From Gagosian et al., 1981b.

1981b, 1982). These authors suggest, on the basis of odd/even carbon concentration ratios and the concentration distribution observed, that the fatty alcohols and the C_{21} to C_{32} fractions of the fatty acid esters and fatty acid salts have a natural terrestrial source, whereas the lighter C_{13} to C_{20} fatty acid esters and fatty acid salts in the Enewetak atmosphere likely have a marine source.

Heavy Chlorinated Hydrocarbons and Other Synthetic Organics

A number of synthetic organic substances were measured in the Enewetak atmosphere, including PCBs and certain pesticides and plasticizers (Atlas and Giam, 1981). The concentrations observed in the vapor phase are presented in Table 14. Concentrations of these substances on aerosols were less than 10% of the vapor phase concentrations. Altas and Giam (1981) point out that rain may not be the primary mechanism for removal of these vapor phase organic substances from the air. Direct vapor exchange with the ocean may be most important. By using a vapor deposition velocity of 8 m h^{-1} for PCB 1242, the direct vapor exchange PCB flux to the ocean at Enewetak would be 35×10^{-10} g cm^{-2} yr^{-1}. This is at least 50 times greater than the precipitation flux of $<0.8 \times 10^{-10}$ g cm^{-2} yr^{-1} for Aroclor 1242, which can be calculated using the concentrations in Table 14 and the annual rainfall amount in Fig. 2a. The vapor phase flux would result in a PCB Aroclor 1242 atmospheric residence time of about 30 days, which would explain the relatively uniform concentration distribution of Aroclor 1242 over the Atlantic and Pacific Oceans and nonurban continental areas (Atlas and Giam, 1981).

Phthalic acid esters are present in rather high concentrations at Enewetak. These compounds are widely used as plasticizers. The concentrations are similar in air over the Atlantic Ocean, the Gulf of Mexico, and in a rural area in

TABLE 14

Concentration of Synthetic Organic Compounds in the Air and in Rain at Enewetak*

Compound	Air concentration, ng m^{-3} Mean	Air concentration, ng m^{-3} Range	Rain concentration, ng l^{-1} Mean	Rain concentration, ng l^{-1} Range
PCB, Aroclor 1242	0.54	0.35 to 1.02	<0.6	
PCB, Aroclor 1254	0.06			
Hexachlorobenzene	0.10	0.095 to 0.13	<0.03	
α Hexachlorocyclohexane	0.25	0.075 to 0.57	3.1	1.3 to 6.8
γ Hexachlorocyclohexane	0.015	0.006 to 0.021	0.51	0.34 to 1.6
Chlordane (α and γ)	0.013	0.006 to 0.015	<0.02	
Dieldrin	0.010	0.006 to 0.018	<0.02	
p,p′-DDE	0.003	0.002 to 0.005	≤0.02	
Di-n-buthyl phthalate	0.87	0.40 to 1.8	31	2.6 to 73
Di-(2-ethylhexyl) phthalate	1.4	0.32 to 2.7	55	5.3 to 213

*From Atlas and Giam, 1981.

Texas, suggesting relatively long atmospheric residence times. Urban area concentrations are about 100 times higher (Atlas and Giam, 1981).

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Chapter 7

Subtidal Environments and Ecology of Enewetak Atoll

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INTRODUCTION

The area of subtidal marine environments of Enewetak far exceeds the intertidal and terrestrial habitats. Subtidal environments are the lagoon and outer reefs and the passages between them which are submerged at low tides. The lagoon and outer reefs are separated, except at passes, by the intertidal reef flat. Although closely connected to the subtidal habitat, the intertidal habitat of Enewetak is not discussed in this chapter except as it relates to circulation, energetics, and processes in the subtidal environment. With an area of about 930 km^2, the lagoon is more than 15 times the area of the intertidal reef flat and 140 times the area of the islands.

The Enewetak Lagoon is relatively deep by atoll standards (Wiens, 1962), with a mean depth of 48 m and a maximum depth of 64 m. Only about 10% of the lagoon is shallower than 18 m, and only 20% is less than 32 m (Emery et al., 1954). The open waters of the lagoon are a voluminous habitat of about 4.2×10^{10} m^2 of water, most of which overlies the deep portions of the lagoon. In both area and volume, the lagoon is the largest subtidal unit at Enewetak. For this chapter, an arbitrary depth of 30 m has been selected to distinguish between the "deep" and "shallow" portions of the lagoon.

The area of the reefs seaward of the reef flat and islands has never been accurately determined. Based on reef widths observed from the air compared to adjacent reef flat widths, the area of the seaward reefs is certainly less than that of the reef flat, perhaps by a factor of up to 3 or 4, but an accurate determination is not presently possible.

The outer slope of the atoll is quite different from the lagoon. The present discussion will include descriptive information on the outer slope to 300 to 400 m depth, but below those depths there is little detailed information concerning the biological communities or geological perspectives.

The subtidal environment of Enewetak contains a number of units, divisible on the basis of location, physical factors, substrate types, dominant organisms, and other factors. Biological communities can be similarly identified. The generally high diversity of marine organisms at Enewetak increases the complexity in describing individual communities and their relationship with the others.

MARINE CONDITIONS

Mean surface oceanic water temperatures at Enewetak range between 27° and 29°C (Atkinson et al., 1981; Coles et al., 1976), with March the coolest month and August the warmest. Temperature extremes during any one month vary about ±1°C from the mean (Coles et al., 1976). Local conditions can alter these, with isolated tide pools in the midday sun reaching the low 40s C.

Typical temperature-depth profiles for the seaward reefs of Enewetak during summer are shown in Fig. 1. From the surface to about 125 m in depth, the temperature gradually decreases from 29° to about 25°C. A slight thermocline begins at about 125 to 150 m, and it changes from 25° to 20°C over a 30 to 40 m increase in depth. At 220 m it is about 13°C with the temperature gradually decreasing to about 9°C at 380 m.

Atkinson et al. (1981) documented the isothermal and isohaline nature of the lagoon water column with no more than a 0.5°C variation in temperature and a 0.20 ppt range in salinity. Almost without exception the shallow waters of the open lagoon and ocean are ideal for eurythermal tropical organisms. The salinity of the lagoon is essentially the same as that of the open ocean. Only in areas of restricted circulation and shallow depth are temperatures elevated significantly above general lagoon water.

The atoll is located in the North Equatorial Current with a general westward movement of water past the atoll. Currents observed on the windward (east) ocean reefs agree with this generalized picture, even at depths of 100 to 200 m, with the ocean current seeming to split north and south near the easternmost extension of the atoll at Ananij. On the ocean side of Enewetak Island, the alongshore component of the current varies in speed but

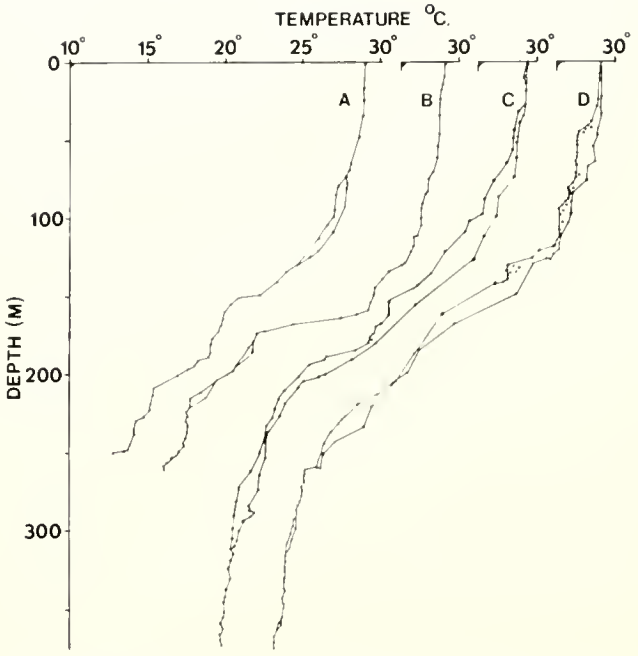

Fig. 1 Temperature/depth profiles from four dives by the DSRV *Makali'i* at Enewetak Atoll, summer 1981. Locations of profiles were as follows: a, Biken, west side of the atoll; b, east side of wide channel; c, Bokandretok, just north of Enewetak Island; and d, Runit Island. Dual tracks represent an ascent and descent profile.

has never been observed to move northward. It is only near passes into the lagoon that tidal currents potentially cause reversal of current direction on the ocean slope of the atoll. On the leeward (west) side of the atoll, currents are variable, and an eddy pattern often seems to exist. At the West Spit, the extreme northwest tip of the atoll, the currents from north and south seem to converge.

Currents in the lagoon and passes are considerably different and are covered in detail by Atkinson et al. (1981) and in Chapter 5 of this volume. In the lagoon the surface current is generally a wind-driven westerly flow with mid-depth return flow to the east. Most water enters the lagoon over the windward reefs and passes out the wide (south) channel. The deep channel has strong tidal flow but little or no net input into the lagoon. Water residence times have a mean of about 30 days but can vary between a few to more than 130 days. The residence time of water in the northern portion of the lagoon is greater than the mean.

The nutrient-poor oceanic water eastward of Enewetak is clear, with visibility normally exceeding 50 m. Such water visibility is typical of windward ocean reefs, but visibility changes when water enters the lagoon over the reef flat. Increased production and suspended particulates reduce the visibility of lagoon waters to 10 to 25 m and occasionally less. Aerial photographs of Enewetak have features on the ocean side reefs visible to depths of about 40 m, although this is limited to a maximum of about 15 to 18 m in lagoon waters. In the northern lagoon, particularly near the islands between Engebi and Bokoluo, two factors may contribute to visibilities at less than 10 m. First, lagoon water residence times in this area are near the maximum, hence high densities of phytoplankton and zooplankton can develop in this water. Second, the presence of fine, easily suspended particulates produced as a result of nuclear tests and cratering in this area may greatly reduce water visibility. Phytoplankton blooms, manifested both as "brown water" and large, thick windrows of extremely dense phytoplankton, have been observed on several occasions in the northwestern lagoon. Visibility in such waters is consequently extremely limited.

Trade wind conditions with steady 10 to 20 knot winds from the east to northeast prevail throughout most of the year at Enewetak. During the summer, trade winds are usually lighter than during the winter, and they can cease for periods of several days. The normal trade winds produce oceanic waves about 1 to 2 m high which hit the windward reef of the atoll. Within the lagoon, the margin on the windward side is relatively calm, being protected by islands and interisland reefs. At high tide, however, much more wave action comes across the reef flat from ocean to lagoon, making conditions choppier on the lagoon margin. The waves which do cross the reef are of small height and wave length, making the surface rough for small boats but having little effect below a few meters depth.

Moving westward across the lagoon, a significant fetch is achieved quickly, and when trade winds prevail, the central and western areas of the lagoon are far from placid. Waves of 1.5 to 2 m with whitecaps can occur, and the lagoonward edge of the leeward reef can have significant surf breaking on it. Significant wave action can also reach the lagoon sides of the islands west of Engebi and the southwestern islands.

The ocean side of the leeward reefs and islands is calm under trade wind conditions with the tide level affecting the wave action crossing the reef from lagoon to ocean. In the lee of islands it is extremely calm for an oceanic area.

Waves in the Marshall Islands as a whole are from the east or northeast, a consequence of persistent trade winds. Waves exceeding 3.5 m high comprise fewer than 2% of waves in the Marshall Islands area (Japan Meteorological Agency [JMA], 1971 to 1978). Waves greater than 3.5 m can occur any time of the year and are generally associated with (1) local storms or typhoons from the east through southwest and (2) more distant northern and southern hemisphere storms. The greatest wave amplitude observed (JMA report) was a long-period 6.5-m swell from the northeast.

Local conditions can also greatly affect wave action. Where tidal currents run against the trade winds, steep standing waves develop. The east channel at Enewetak can be treacherous under strong trade winds with the tide dropping sharply. A distinct central tongue of breaking waves extending out the channel to the ocean is visible from the air under these conditions. Similarly, the west

side of the wide passage is an area of merging waves from the lagoon and refracted oceanic waves and swell with strong southerly currents producing standing waves and short, steep seas.

During summer calms and at odd times during the rest of the year, the lagoon and surrounding ocean become smooth. At such times it is possible to swim off the reef flat to the windward ocean reefs because the surf is small and gentle. Surface slicks are found in lagoon waters. The windrows of phytoplankton from blooms have been found during such calm periods.

Swells from distant storms create a different situation in which shores exposed to the swell (which can be either windward or leeward) are heavily pummeled, whereas the waves produced by wind in the immediate area may be small. Most impressive are those rare times when large swells thunder against the reef while calm trade winds produce an almost mirror-like surface elsewhere. On shores normally lacking high surf, these waves can cause considerable damage. Such swells can also enter the lagoon through the southern pass to break on the lagoon shore of Enewetak, Medren, and other islands.

Several typhoons and near-typhoon strength storms have passed by or over Enewetak during the last decade. Although the atoll is generally not considered in the typhoon belt, these storms have had a significant and readily visible effect on Enewetak reefs. Often a storm whose center does not pass especially close to Enewetak can produce storm waves which severely damage reefs, although above-surface damage from winds may be very light.

Deep Lagoon Biological Communities

The lagoon bottom below 30 m depth consists largely of soft substratum with small to large reef structures (pinnacle reefs) spread randomly throughout the area. Except for the pinnacle reefs, relatively little published information exists regarding in-situ observations of either the lagoon slope or deep lagoon benthic biological communities or geology. Nearly all published information is based on surface-lowered grab samplers or dredges. Emery et al. (1954) reported on results of samples taken by an "underway" bottom sampler and about 50 photographs taken by a remote camera at unspecified locations in the deeper lagoon. More recent researchers (Nelson and Noshkin, 1973; Noshkin, 1980) have relied on grab samplers or short-core samplers to obtain bottom samples for analysis.

The only published in-situ observations of the deep lagoon are those of Gilmartin (1960), made during deep scuba dives on a transect across the southern lagoon. Twelve of these stations were below 30 m in depth. All stations below 30 m had coral patches present within the range of visibility; these varied from only a few small heads in one instance to massive patch reefs rising 15 m or more above the surrounding bottom. Some stations had the substratum covered with "mounds of sand and castings," but for most of the deeper stations, the presence or absence of mounds was not noted. This study confirmed that abundant algal communities exist in the deep areas of Enewetak Lagoon, many occurring at the deepest depths reached (62 m). Coral patches at these depths seemed more densely populated with algae than adjacent sand. Eight species of *Halimeda* were found primarily between 42 and 62 m, supporting previous reports that the genus was "most common and luxuriantly developed at the deeper levels." Gilmartin (1960) was the first person to realize the intense bioturbation of the soft substrate bottoms of the lagoon, commenting that "the continual 'churning' of the substratum by these benthic organisms has prevented algae, which might occur elsewhere on the same stations, from starting and growing to the point where they would not be 'uprooted' or buried by the sand displacements."

During 1980 and 1981, a distributional survey of deep lagoon benthic communities was conducted using a lowered camera system. During this "Enewetak Benthic Survey" over 2000 photographs covering 24 m^2 each were taken at 190 stations throughout the deep lagoon (Colin, 1986). Additionally, in the summer of 1981 the submersible *Makali'i* was utilized for a series of dives in several areas of the deep lagoon to augment the photographic survey.

STATE OF KNOWLEDGE OF SUBTIDAL MARINE ENVIRONMENTS

With certain exceptions, the subtidal marine environments of Enewetak cannot be characterized as well known. Often our knowledge is based on studies in the southern lagoon close to the lee of the southern islands. The distances from support bases, the generally rough conditions of the lagoon outside protected lee areas, and the rapidly increasing water depth have severely limited work in both the northern and central lagoon. Much of the work accomplished in the southern lagoon is of equal applicability to the entire lagoon, but differences do exist between these areas.

Even the southern areas of the lagoon below 20 to 30 m depth are poorly known. This is due to the limited access of scuba-diving scientists to the deep lagoon bottom, particularly at its most common depths of 40 to 60 m. Although a few hardy souls have ventured to dive in these areas, working time is limited, nearly precluding studies providing an understanding of overall conditions in the deep lagoon. Significant work on the deep lagoon floor requires either specialized instrumentation and recording methods or suitable vehicles for in-situ work.

The present work is intended to provide descriptive information about subtidal habitats in the following order: (1) deep lagoon; (2) shallow lagoon; (3) lagoon–ocean passes; and (4) the seaward reefs, from the center of the lagoon outward. The information has been drawn from publications, annual reports, unpublished information in

MPRL files, and unpublished data from numerous scientists.

No comprehensive descriptive account of the subtidal environments of Enewetak has been attempted. Only a few specialists have endeavored to discuss atoll-wide distribution and contributions of their restricted groups of organisms. Cuffey (1973 to 1978) examined the role of bryozoa at Enewetak with comparison to other reef areas. He listed three major marine benthic "macrohabitats" at Enewetak: the coral-dominated, the bedrock-dominated, and the sediment-dominated. He distinguished between "larger patch reefs (from 25 to more than 150 ft height)" and "smaller coral knolls (from 1 to 25 ft high)" in examining bryozoan distribution at Enewetak. He also distinguished between bioherms ("coral-dominated macrohabitats with significant height") and biostromes ("coral-dominated macrohabitats lacking significant height"), such as his "coral pavement."

Allen (1972), in his work on anemonefishes, provides brief descriptions of some Enewetak habitats. The major physiographic features of environments from outer reef slope, reef flat, shallow lagoon margin, and deep lagoon are mentioned. He thought that the deep lagoon floor "appears to be of a fairly uniform nature" and had "large stretches of sand with occasional small patch reefs." Deep lagoon pinnacles were described as "an oasis, rising from the barren lagoon floor" and harboring "an extraordinary wealth of marine organisms."

The deep lagoon can be characterized as dominated by sediment substrates but with reefs of widely varying size and vertical relief, distributed fairly evenly throughout the lagoon. The soft substrate supports several different biological communities, often occurring within short distances of other soft substrata and reef substrata. Extensive disturbance of the sediments is evident in many of the benthic photographs and from submersible dives.

Based on point counts of the benthic survey photographs, approximately 85% of the deep lagoon has soft substrata, with the remaining 15% hard substratum. Nearly half of the stations had 100% coverage of soft substrata, more than 60% were 90% or more soft substrata, and more than 75% were 75% or more soft substrata coverage. If the individual photographs are considered, rather than entire stations, slightly higher percentages of 100% and 90% soft substrate coverage are found.

The soft substrate biological communities comprise four identifiable types. These include (1) open sand substrate without a visible algal mat, (2) sand substrate with visible algal mat on its surface ("algal film"), (3) sand substrate with macroalgae, particularly species of *Halimeda*, on its surface ("algal flat"), and (4) sand with large populations of an unattached Fungiid coral, *Cyclosersis* and *Diaseris* spp. ("button corals"). Typical views of these communities from benthic survey photographs are shown in Figs. 2 and 3. Interpretation of the benthic survey photographs has been facilitated by observations and photographs from the Enewetak submersible project and scuba dives in shallower areas where similar communities occur.

The soft substrate communities often intergrade, for example, the macroalgae of the "algal flat" community decreasing in density until only open sand remains. Arbitrary points at which one community "becomes" another have been used in interpreting the photographs, but absolute distinctions among types of soft substrate communities are often impossible. The distributions of community types in the deep lagoon as based on benthic survey photographs are shown in Figs. 4 and 5.

Deep lagoon sediment substrata with no visible algal cover are qualitatively similar to areas of the lagoon margin as shallow as 15 m. They are usually heavily bioturbated, dominated by the conical mounds produced by callianassid shrimp. The occurrence of open sand substrates, based on benthic survey photographs, is shown in Fig. 4. Although this covers only a limited number of stations, it does indicate "barren" soft substratum can occur throughout the lagoon. Open sand substratum, however, can change within a few meters horizontally to soft substratum covered with macroalgae. Such short-scale horizontal changes among soft-substratum communities and hard substrata are common throughout the lagoon.

It is possible that the rapid sediment turnover in open sand areas is responsible for the lack of dark algal films of macroalgae. However, algal mats over 1 m in diameter do occur in heavily bioturbated areas but are capable of forming in only a few days time. Biological sediment overturn is concentrated at specific points in the short term (days) producing "splotching" of algal mats when viewed from above. Other factors affecting density of algal films (nutrients in water or sediment, water clarity, standing crop already present, etc.), may be critical in controlling the presence of dense algal mats.

The presence of algal films, particularly diatoms and blue-green algae, on sand bottom without visible algal mat is well known (J. T. Harrison, personal communication). The population level at which an algal mat becomes visible in a photograph or to a human observer is dependent on the standing crop per unit area and the plants involved.

Water visibility over open sand bottoms is often limited to only 5 to 10 m, even in the deep lagoon. Considerable amounts of suspended particulates were observed from the submersible *Makali'i*, using its lights, in the deep lagoon; but relative densities varied considerably from day to day at one location. It was noted, however, that suspended particulates were often elevated closer to the bottom than near the lagoon surface. Similar observations commonly have been made by scuba divers over open sand substrates at depths around 20 m.

Sediment will often have a clearly visible thin layer of microalgae on its surface. Algal films are seen in the lagoon margin areas as shallow as 15 m. At depths of 15 to 30 m, small dense algal mats (only a few centimeters in diameter) are often seen on otherwise clear bottoms. Where a film of algae exists, any recent disturbance of the sediment is clearly indicated by lack of, or disturbance of, the algal mat. This relationship has been closely examined at diving depths from 15 to 30 m and has been verified in

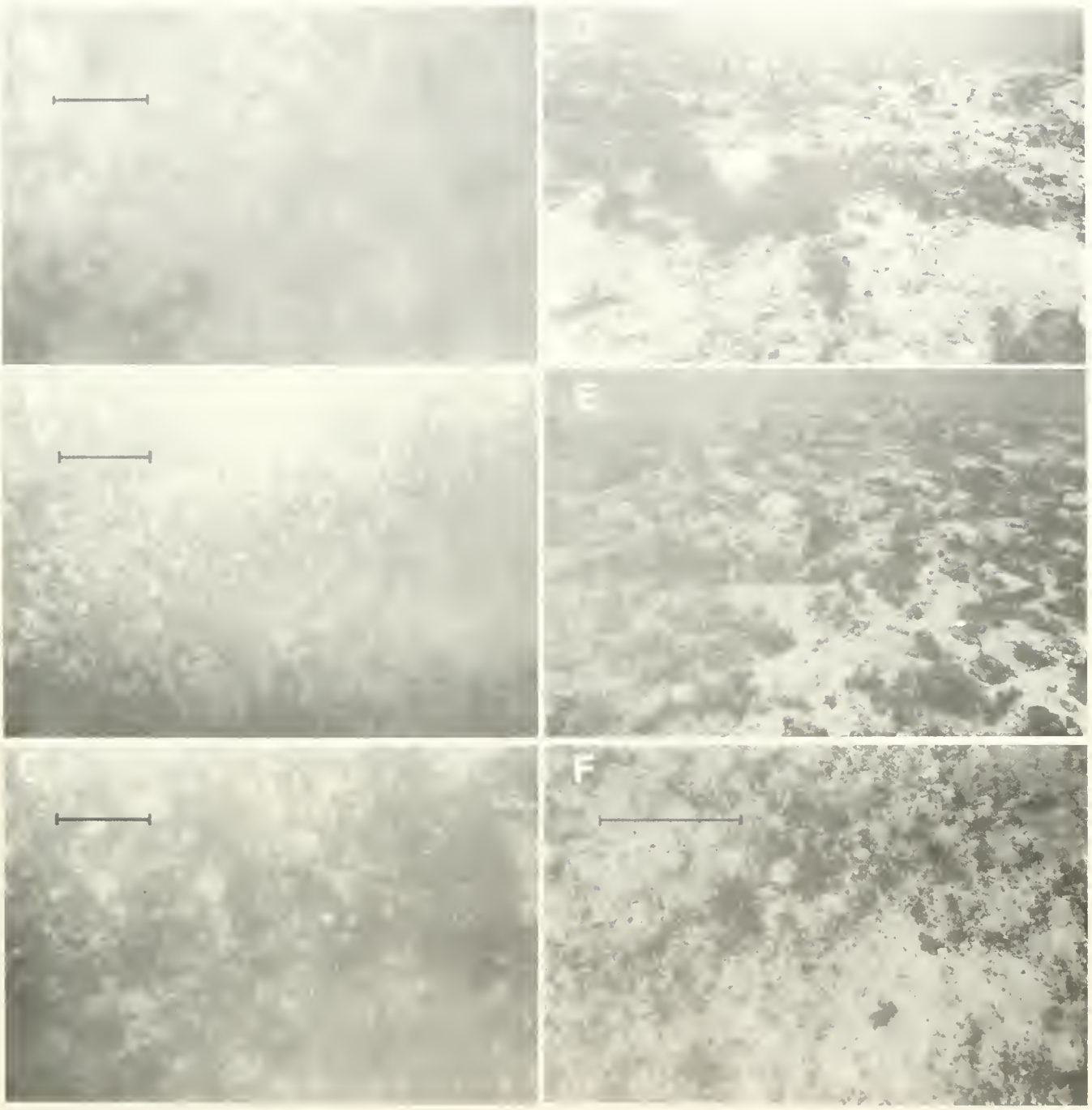

Fig. 2 Enewetak deep lagoon soft bottom communities. Bar equals approximately 1 m. a, Algal film community photographed by vertical benthic camera. Considerable bioturbation (pale splotches) is visible in this photograph (56 m depth); b, Algal flat community, vertical benthic camera, dominated by species of *Halimeda* (51 m depth); c, Algal flat community dominated by mixed macroalgae, vertical benthic camera (55 m depth); d Algal flat community at 57 m depth, central lagoon, dominated by mixed macroalgae, with small *Halimeda* sp. thalli. Some mounds produced by bioturbation are visible (diver photograph); e, Same general area as above with sponges (dark objects near center), *Halimeda* sand and abundant macroalgae visible, 57 m depth (diver photograph); f, Near vertical view of area of Fig. 2d and 2e, 57 m depth. Significant bioturbation is evident in this diver photograph. [Figures from Colin, 1986.]

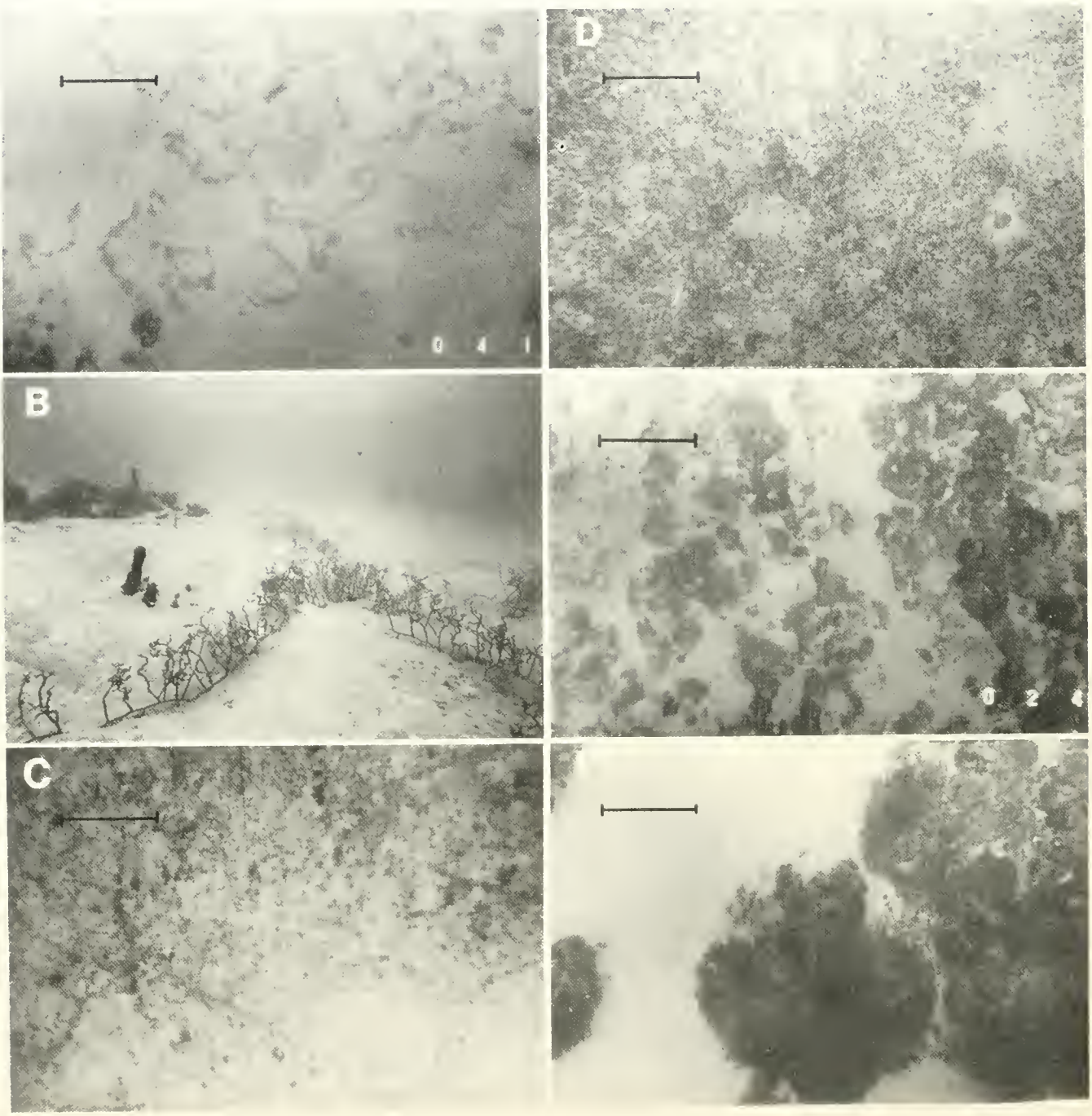

Fig. 3 Enewetak deep lagoon communities. Bar equals approximately 1 m length. a, Algal flat community dominated by *Caulerpa*, vertical benthic camera photograph (51 m depth); b, Oblique view of sediment bottom with *Caulerpa* sp. and small patch reefs in left background, 44 m depth. Note the mounds produced by callianassids on sediment. Diver photograph; c, Benthic community with "button corals" and *Caulerpa* algae, vertical benthic camera (55 m depth); d, Dense "button coral" community (Cycloseris and/or Diaseris) at 56 m depth, vertical benthic camera; e, Hard substratum community with relatively barren rock surfaces, vertical benthic camera (44 m depth); f, Hard substratum community with patch reefs with stony corals and gorgonians, vertical benthic camera (47 m depth). [Figures from Colin, 1986.]

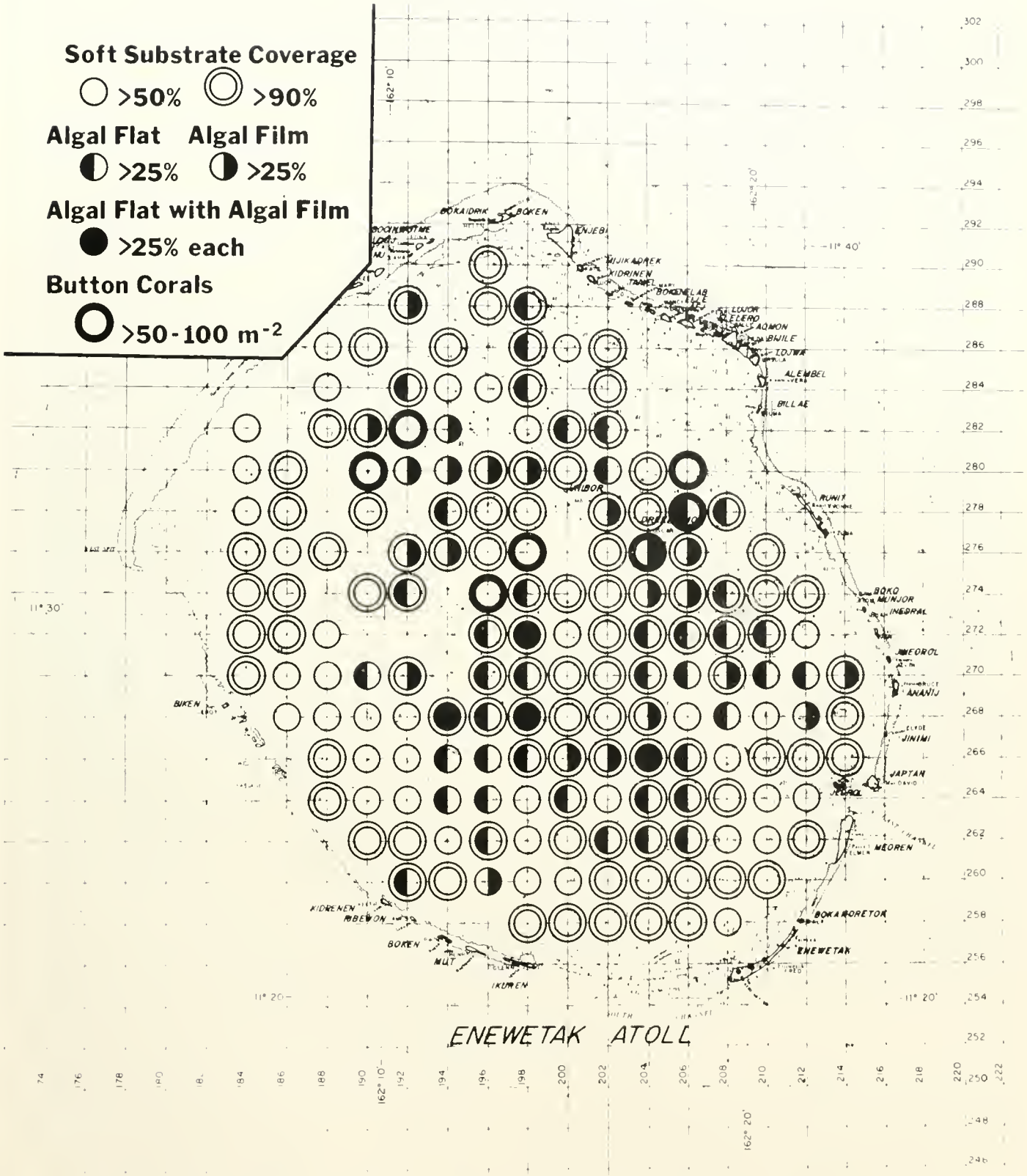

Fig. 4 Distribution of soft substratum communities at benthic photographic station in the deep lagoon (<30 m depth), Enewetak Atoll (Colin, 1986).

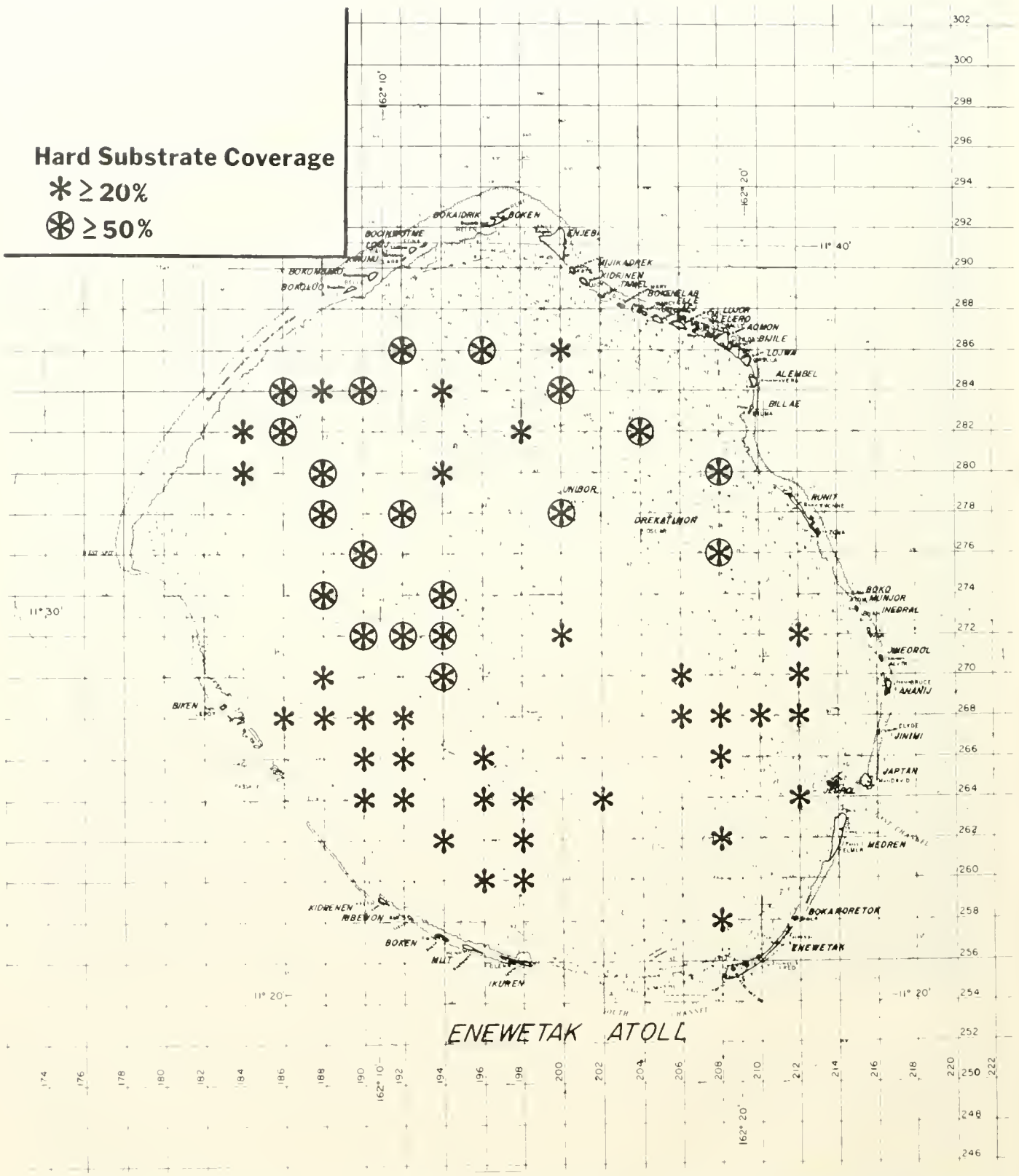

Fig. 5 Distribution of hard substratum communities at benthic photographic stations in the deep lagoon (<30 m depth), Enewetak Atoll (Colin, 1986).

the deep lagoon by observations and photographs from the *Makali'i*. Such areas appear much lighter when viewed from above because the algal mat has not had time to regrow. The distribution of stations with over 25% algal mat is shown in Fig. 3.

Algal flats are dominated by macroalgae, particularly species of *Halimeda* and *Caulerpa*. Algal films can also occur with macroalgae. Individual plants are often separated by areas of open sand, but densities can be high enough that relatively little sediment bottom is visible. *Caulerpa* sp. grows via rhizomes, spreading out over the bottom in easily distinguishable patterns.

Areas of algal flat can range from a few meters to over hundreds of square meters. On benthic photographic traverses of large algal flats, decreasing density of thalli on their edges was often seen grading into open sand. The situation also exists where dense macroalgae changed abruptly into open sand. The distribution of stations with more than 25% algal flat is shown in Fig. 4.

The algal flat community is a diverse soft-bottom community with many epiphytic organisms with an apparently higher biomass than open sand and algal films. A shallow-water algal flat community, dominated by *Halimeda* spp., occurs as shallow as 18 m and is a shallow lagoon community accessible to divers, comparable to the algal flat of deeper water. Termed "*Halimeda* meadows," these algal communities extend shallower than the 30 m arbitrary cutoff in the "deep" lagoon, but because of strong similarities these are considered representative of deep lagoon *Halimeda* communities. These consist of extremely dense stands of *Halimeda* spp., associated with other abundant macroalgae, which often form distinct circular or irregular algal communities from a few to many tens of meters across. The meadows are often a slightly elevated mound, perhaps 1 to 3 m higher than surrounding sediment bottoms. Some stony corals, principally finely branched *Acropora* and small head corals, often occur on the mound. The skeletons of these combined with *Halimeda* and other calcareous algae plates produce a higher percentage of coarse material in the surface sediment than in surrounding open sediment areas. The elevation of the *Halimeda* mound is probably due to accumulation of carbonate material produced at the mound, whereas adjacent sediment areas have not kept pace with the relatively rapid carbonate accumulation on the mounds. Information is lacking concerning the growth and longevity of *Halimeda* mounds; such information would be of particular interest. The mounds/meadows are also foci for high animal abundance. Small fishes, particularly herbivores and bottom feeders, are abundant, as are benthic invertebrates. Preliminary production/respiration data (MPRL, 1981) indicated that in spite of high algal biomass there is little or no net productivity by the *Halimeda* mound community, the production of the high algal biomass being usurped immediately by resident animal populations.

A community of small corals of the genera *Cycloseris* and *Diaseris* growing unattached on sediment substrates has been found in the deep lagoon (Colin, 1985). In this community, the small (2 to 6 cm) corals, called "button corals," occurred in densities of up to 100 m^{-2} and were photographed at only six benthic stations (Fig. 4). All these were in the deeper portions of the lagoon below 50 m. The photographs at that station were all, or nearly all, of *Cycloseris*- and *Diaseris* spp.-dominated bottom. Obviously beds of this coral can cover areas many hundreds of square meters. Also, macroalgae—particularly species of *Halimeda* and *Caulerpa*—small sponges, and other invertebrates often occurred among the button corals.

Some elements of the fauna of soft substrata at diving depths at Enewetak are fairly well known. In the case where species occurring at Enewetak are documented, other biological information is usually not known. In one of the few instances where more than the base essentials are known, several species of irregular sea urchins occur buried in, or on, sediments. The density of given species in apparently similar areas of the lagoon margin has been documented to vary by well over an order of magnitude (V. S. Frey, unpublished data). Similar population variation has also been observed at a single station over several months. Although these variations have been documented, the many factors determining population structure of infaunal organisms are poorly understood.

The smaller organisms dwelling in sediment bottoms are more poorly known. For example, using a technique where an area of bottom is covered by a plastic sheet and rotenone, or another toxicant, introduced beneath the sheet for a time, lancets (Branchiostomidae) have been collected recently at a density of approximately 100 individuals m^{-2} on sediment bottoms below 15 m at Enewetak (Suchanek and Colin, 1986). Schultz et al. (1952), in spite of their collecting efforts in the Marshall Islands, took only a single specimen of lancet at Bikini Atoll. Approximately 50 small unidentified ghost shrimps were collected per square meter using this technique, a density far greater than imagined. The only visible evidence for the presence of these small callianassids is small-scale conical mounds present in combination with larger mounds produced by larger species. Also collected were stomatopods, sipunculids, molluscs, and echinoids (Suchanek and Colin, 1986). Interestingly, in sediment-leveling experiments the number of small-scale mounds (less than 5 cm diameter) was an order of magnitude or more greater than large-scale mounds, supporting evidence of the high populations of small callianassids (Suchanek et al., 1986).

Pinnacle Reefs of the Deep Lagoon

It is impossible to draw an absolute line where the patch reefs on the margin of the lagoon and pinnacle reefs begin. A working distinction can be made between "patch reefs" which rise from a surrounding sediment or rock bottom which is visible from the surface under normal conditions and "pinnacle reefs" rising from depths where the

surrounding bottom is not visible. Emery et al. (1954) used the term "coral knoll" for such structures, but this author thinks it is not truly a descriptive term in this case.

The pinnacle reefs of Enewetak Lagoon cover only a small percent of the bottom area but are areas of great biological diversity and interest. Their presence in the deep lagoon, appearing as light areas among the dark waters, parallels on a smaller scale the presence of atolls in the deep ocean. Pinnacle reefs vary greatly in size, from a few tens of meters to over 1 km in diameter at their base. Emery et al. (1954) pointed out that among the 20 largest pinnacle reefs, they are quite evenly spaced throughout the lagoon. For several reasons the distribution of smaller pinnacles, though, is not as well known. The tops of most are not visible from the surface and because of their small size, they are easily missed by echo sounding surveying. Emery et al. (1954) estimated there were about 3000 coral pinnacles in the Enewetak Lagoon but ignored any which did not have a relief of more than 4 m. There are about 150 to 180 pinnacles which should be visible from the surface (<18 m depth), rising from depths of about 35 m or more.

The surface-visible pinnacles are the best known because they can be located relatively easily for diving and are shallow enough for prolonged scuba diving. They have been used as sites for a variety of studies, but their origins and underlying structure are not well known.

The slope of the sides of pinnacle reefs can vary greatly. In general, the smaller a pinnacle reef diameter, the steeper its slope. On small pinnacles much of the slope is nearly vertical. The largest pinnacles are somewhat flat on top for much of their diameter but still slope to the lagoon floor at an angle of at least 10 to 20°.

Those pinnacles closest to Enewetak Island are best known because of their closeness to MPRL. Figure 6 indicates the location of many of these and the names applied to them. There is, however, considerable variation in the biological communities between pinnacles, even among those of similar size and shape. A few pinnacle reefs are described subsequently in greater detail.

An example of a well-developed small, but not typical, pinnacle reef is "Pole Pinnacle," so named because of a toppled marker pole and anchor block on its upper surface. It is located 1.6 km from Jedrol Island (Fig. 6). Pole Pinnacle actually rests on the edge of the deep channel on an extension of the wedge of shallow reef produced by the split of the deep channel west of Jedrol. The entire upper surface of the pinnacle is dominated by the coral *Porites rus*, the *P. iwayamaensis* of Wells (1954) (Veron and Pichon, 1982). On the upper surface at 3 to 5 m depth, the columnar form of *P. rus* occurs, but on the sides of the pinnacle where *P. rus* also dominates, the plate-columnar form occurs. The vertical distribution of *P. rus* varies on different sides of the pinnacle. On the northern face, little occurs below 8 m, whereas on the south side a solid cover is found above 12 m. The eastern face has its first colonies of *P. rus* at about 26 m, with large patches starting at 18 m. The western face has some large clumps as deep as 15 m. Below the steeply sloping upper portion, the bottom becomes less steep, having an angle of about 45° to depths of 30 m. The bottom around the base of the pinnacle becomes relatively flat with coarse *Halimeda*-dominated sediment and occasional small reefs. On the eastern side, which abuts the side of the deep channel, the bottom slopes away farther to about 40 m.

Below the depth of *P. rus* dominance, the coral cover is low. The bottom is largely rocky substrate with shelves on which considerable quantities of sediment are retained. Hillis-Colinvaux (1980) reported that Pole Pinnacle "possessed the same high *Halimeda* species richness" encountered in some shallow water interisland channels. She felt the *Halimeda* species populations of the sides of all pinnacles "may well be principal suppliers of carbonate to the reef floor." In light of recent information on "*Halimeda* meadows" and the occurrence of *Halimeda* in the deep lagoon, pinnacle reefs may be less important as carbonate producers than previously suspected, but they are still significant. Both small and large pinnacles are definitely *Halimeda* spp. sediment source points; their sloping sides and shallow depths producing a potentially radial dispersal of *Halimeda* plates from shallower depths to the deep lagoon.

A well-known example of a "larger" pinnacle reef is South Medren Pinnacle, located 1.7 km west of the south end of Medren (Fig. 4). It is about 100 m in diameter, roughly circular, and slopes off at about a 30° angle to the lagoon floor at 35 to 40 m. Its upper surface is rugged, with coral ridges and heads interspersed with deeper rubble areas. Coral coverage is not as high as Pole Pinnacle but seems average (10 to 30%) for most pinnacle reefs.

Coral distribution on the tops and flanks of pinnacles, particularly larger ones, seems somewhat patchy (Fig. 7). Definite sediment downfall areas exist on large pinnacles which restrict corals. Medren Pinnacle has several on its southern face, and near the base of the pinnacle at 35 to 40 m only isolated areas of reef exist. These small patch reefs are generally of low relief, somewhat rounded with abundant macroalgae populations. Here the large blue tubular to vasiform sponge, *Cribochalina olemda*, is often common.

Gilmartin (1966) found the green alga, *Tydemania expeditionis*, along with species of *Caulerpa*, *Halimeda*, and *Dictyota* to form the bulk of algal biomass on the deep lagoon coral patches at depths greater than 40 m. Previous dredging work on *T. expeditionis* had indicated it to be uncommon, but Gilmartin (1966) found it to be first or second in abundance among algae on deep lagoon coral patches, equal to or exceeded only by *Halimeda* at 51 to 62 m depth.

Ship Channel #1 Pinnacle (not shown in Fig. 6), located some 6 km west of Ananij Island, is unusual. It is a fairly small pinnacle, about 100 m in diameter, rising within about 3 m of the surface with the lagoon about 40 m deep around it. The eastern end of its top is dominated by *Porites rus*, similar to that found at Pole and Tunnel Pinnacles, while its western end has almost exclusively table *Acropora* corals and appears to have been devastated by a storm several years ago.

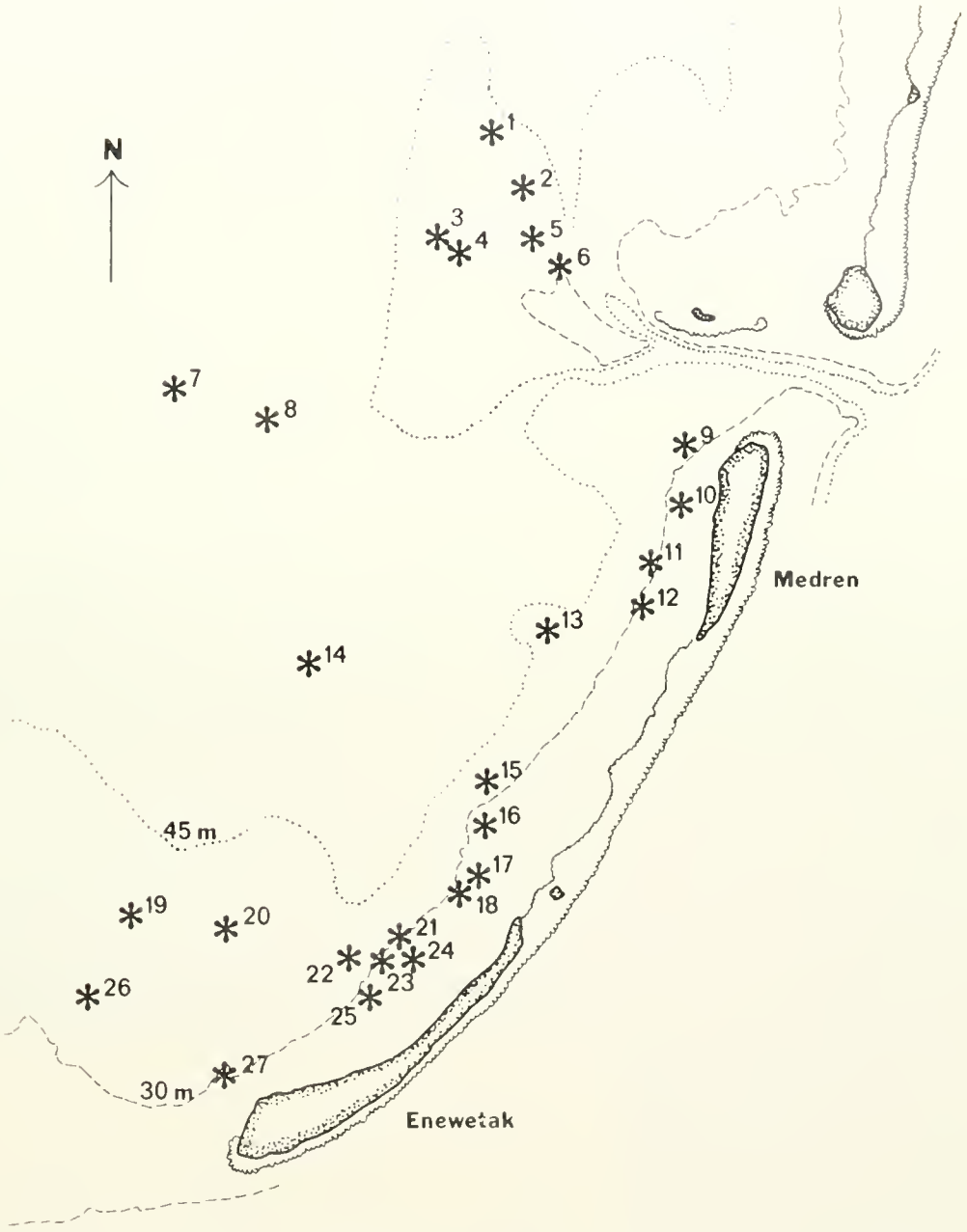

Fig. 6 Locations of lagoon pinnacle reefs in the southeastern portion of Enewetak Atoll. Many of these pinnacles have been important collection localities and are not named on any other published charts. Names used are as follows: 1. Tunnel Pinnacle, 2. unnamed, 3. unnamed, 4. Cucumber Patch, 5. Dead Pinnacle, 6. Pole Pinnacle, 7. unnamed, 8. unnamed, 9. unnamed, 10. unnamed, 11. unnamed, 12. Medren pseudopinnacle, 13. south Medren Pinnacle, 14. Reefer 8, 15. Sand Island #1, 16. Sand Island #2, 17. north Enewetak Pinnacle, 18. Marine Pier Pinnacle, 19. unnamed, 20. unnamed, 21. Harry's Patch, 22. Gemini Pinnacle, 23. Power Plant Pinnacle, 24. Friendly Fish (Bubblebut), 25. Mini Power Plant Pinnacle, 26. unnamed, 27. Garbage Pier Pinnacle.

Asparagopsis taxiformis is perhaps, after *Halimeda* spp., the most common algae on pinnacle reefs (Fig. 7). Its upright thalli protrude from most rocky areas, often in dense stands. Schleck (MPRL, 1978) found that *A. taxiformis* grew in a band about 1 m wide and several hundred meters in length along leeward island lagoon shores. In deeper water, Schleck reported it formed an abundant, but scattered, community with a vertical distribution to at least 20 to 30 m.

The Lagoon Margin

The lagoon between 30 m depth and the shore of islands or the reef flat, the "lagoon margin," is an area of

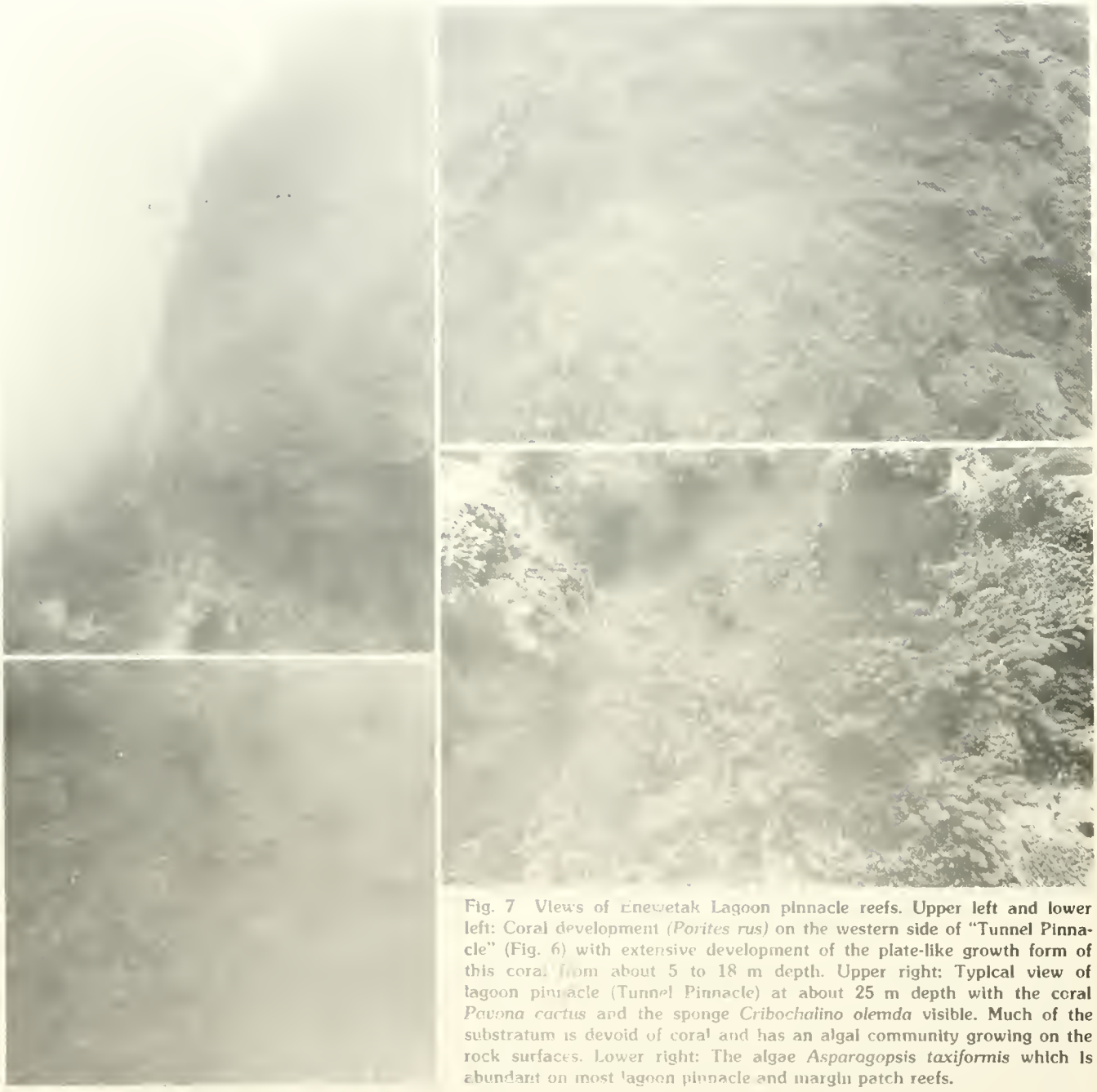

Fig. 7 Views of Enewetak Lagoon pinnacle reefs. Upper left and lower left: Coral development *(Porites rus)* on the western side of "Tunnel Pinnacle" (Fig. 6) with extensive development of the plate-like growth form of this coral from about 5 to 18 m depth. Upper right: Typical view of lagoon pinnacle (Tunnel Pinnacle) at about 25 m depth with the coral *Pavona cactus* and the sponge *Cribochalino olemda* visible. Much of the substratum is devoid of coral and has an algal community growing on the rock surfaces. Lower right: The algae *Asparagopsis taxiformis* which is abundant on most lagoon pinnacle and margin patch reefs.

great transition. The width of the lagoon margin varies considerably from only a few hundred meters at the south end of Enewetak Island to over 1 km from Lojwa north to Engebi and Boken. The deeper portions are similar to the deep lagoon, and because of their accessibility to scuba divers, are an excellent area for studies relevant to the deep lagoon. From about 6 m to 15 to 20 m depth, the bottom has areas of relatively steep sediment slopes, often at the angle of repose; abundant patch reefs, often with relatively high vertical relief, high coral diversity, and abundant fish populations.

The windward lagoon margin is strongly influenced by the reef flat. Areas of high water transport across the reef flat ("rips"), found at the ends of islands and also along interisland reef flats, affect the distribution of sediments and patch reefs on the lagoon margin. In the lee of the large islands (Enewetak, Medren, Runit) patch reefs are somewhat "dead," with relatively low coverage of corals.

A different situation exists on the lagoon margin on the southwestern, western, and northwestern sides (leeward). Because of exposure to prevailing winds across the fetch of the lagoon, these areas often possess an almost barrier-reef type structure with small patch reefs inside it. The sediment bottom often slopes upward steeply near this structure. This is discussed subsequently.

Hiatt and Strasburg (1960), in their classic study of reef fish feeding ecology, presented a brief summary of Enewetak reefs. They reported that in the lagoon "in protected areas there is a discontinuous series of irregular patch reefs which extend from nearshore to the outer reef slope leading to the deeper parts of the lagoon." On the western side of the lagoon, "the lagoon reefs are better developed and frequently are continuous, because they receive fairly strong waves engendered by the prevailing winds" across the lagoon. In some respects, they come to resemble reefs of the windward shore. Hiatt and Strasburg (1960) provide drawings of typical reef environments (tidal pools, seaward reef flat, spur and groove surf zone, patch reefs and coral heads, mid-water) with the characteristic fishes found there.

The patch reefs of the windward lagoon margin have particularly well-developed coral communities where the water flow across the reef is unimpeded by islands. The vertical relief of the reef generally increases with size, but in many cases small reefs have a relief about one-half their diameter, up to a maximum of about 6 m relief. Table *Acropora* sp. corals are abundant on these patch reefs, whereas other corals grow well on the sides of the patch reefs and even under overhangs because of the reflection of light from the white bottom. Relatively few soft corals occur in such areas.

Sand areas in between the lagoon rim patch reefs are areas of high grazing pressure by surgeonfishes and parrot fishes. Burrowing activity in the sediments is also high, mainly through the activities of a variety of fishes.

An important factor determining the distribution of windward lagoon margin patch reefs is the effect of lagoonward sediment and rubble movement from the reef flat. Between Enewetak and Medren such patches are abundant, but they are best developed in areas protected from sediment "overwash." Leeward of Bokandretok is an area of numerous patch reefs, whereas north and south of this the island rips have covered the area with sediment where the reefs occur. Farther north along the reef, areas of sediment overwash have at best reduced numbers of patch reefs. In areas protected by structures diverting the cross-reef flow of sediment, patch reefs are better developed, coming close in behind the reef flat. Nolan (1975) used a large series of patch reefs in the lee of "Isaac's Island," a small rock and sand spit, for his fish community studies.

Nolan (1975) described some patch reefs between Medren and Enewetak Islands where he analyzed and manipulated reef fish populations on these and artificial reefs. He felt coral development was particularly luxurious on the patch reefs on the lagoon side of Isaac's Island. Nolan (1975) pointed out that many of the patch reefs to leeward of Enewetak and Medren Island were predominantly dead coral. He provided a detailed map locating his study reefs and chose reefs of about 3 × 3 × 3 m in size, which were abundant, in depths of 5 to 7 m. He noted that the reefs in the lee of Isaac's Island were protected from the full brunt of the cross-reef currents but that an eddy pattern existed on the leeward side of this small outcropping which provided abundant water circulation.

Nolan's (1975) study reefs were predominated by massive "table" *Acropora cythera*, but during his study in 1972, heavy surge from the leeward side of the atoll dislodged many of these corals on his study reefs. Sand in this area was also removed and deposited in shallow water creating a 3 m high sand bar continuous from Medren to Enewetak. This sand ridge was destroyed and moved into the lagoon with the resumption of normal trade wind weather and sea swell.

Similar destruction of *A. cythera* on patch reefs was observed during southwesterly to westerly storms in March 1981 and July 1982. The tables of *A. cythera* were broken loose at their bases and moved. Many specimens ended up on island beaches with the corallum nearly intact, testament to the strength of this form.

North from Japtan to Ananij, no significant lagoon margin patch reefs exist between islands. The bottom slopes relatively steeply into the lagoon, and the reef from ocean to lagoon is narrow. The zonation across the reef is distinct (Fig. 10) and is described subsequently. Chinimi, the only island interrupting this 4 km stretch of open windward reef, has the lagoon margin protected from reef flat "outwash," and patch reefs are well developed in the lee of the island. The change in zonation of the lagoon margin is really visible north from Japtan. Island rips occur north and south of Chinimi and lagoonward depth contours veer close to Chinimi's shore in its lee. This cusping of the atoll rim behind islands is seen in other areas of the windward side. The area on the northern lagoon margin of Chinimi has one of the best developed reefs along the shore of any windward island, with lovely microatolls, although less than 100 m north the reef seems limited by the island rip and sediment outwash.

Ananij similarly has a large number of lagoon margin patch reefs in its lee and has the most developed island rip system of any island at Enewetak. Between it and Runit, 8 km farther north, cross reef zonation is similar to that south of Ananij, but more islands are found on the reef. The island cusping effect, however, is evident with many patch reefs in their lee.

A good example of a well-developed lagoon margin patch reef is "Choptop Reef," located just north of "Isaac's Island" between Enewetak and Medren (Fig. 8). It is large for a lagoon margin patch reef, but smaller reefs adjacent to it are similar and provide easy comparison. Choptop has high coral cover and diversity and high fish populations (Fig. 8). It is located on the margin of a reef flat rip, and although not in the strongest portion of the current coming off the reef flat, it is in a well-flushed area. An

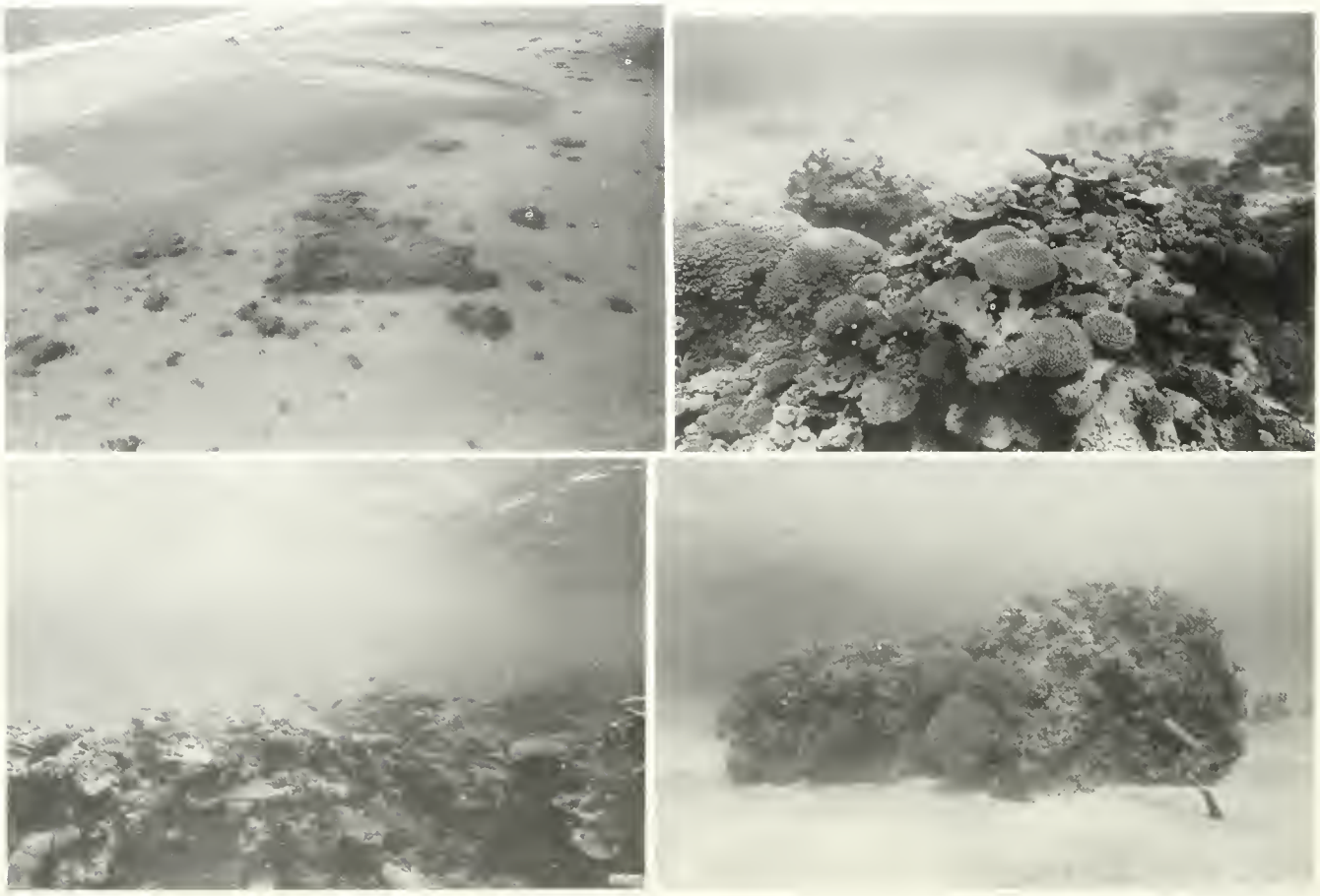

Fig. 8 A lagoon margin patch reef, "Choptop Reef," from the air. The main reef (center of photograph) is surrounded by smaller "Satellite Reefs," some of which are *Porites cylindrica* colonies probably broken from the main reef by storm waves. The reef flat is seen in the upper left with a sediment/rubble bar, produced by a cross reef "rip" seen in the upper center. Water depth around Choptop Reef is about 6 m. Upper right: Typical view of coral development on a lagoon margin patch reef (Choptop Reef) with the sediment floor surrounding the reef visible in the background. Lower left: View of upper surface of a lagoon margin patch reef (Choptop Reef) with abundant coral and fishes visible. Depth on the top of the reef is approximately 2 m. Lower right: "Satellite Reef" located about 15 m away from the main portion of Choptop Reef. This reef is simply a smaller version of Choptop with a vertical relief of about 4 m.

aerial photograph of the reef is shown in Fig. 8, with the rubble bar and outwash area of the reef flat rip clearly visible.

There are several smaller "satellite" reefs close to Choptop which may have resulted from storm fragmentation of the larger reef (Fig. 9). The sediment around lagoon margin patch reefs, like Choptop, is coarse. Calcareous macroalgae, such as *Halimeda* spp., occur sporadically on the lagoon margin (Fig. 9), not in large beds as is found in the deeper lagoon.

Coral heads on the upper surface of lagoon margin patch reefs often rise to near the surface, but at Enewetak, patch reefs are not planar at about mean to low water levels. At Ujilang Atoll, 200 km southwest, lagoon patch reefs were planar on top, reaching low water level, because of growth of coralline algae. Enewetak patch reefs lack abundant coralline algae on the upper surfaces which may account for these differences. Encrusting corallines are abundant within interstices of Enewetak patch reefs, but the difference, compared to Ujilang, in the amount of exposed corallines is striking.

Where the internal structure of patch reefs is exposed, such as in caves or recent fractures, it appears to be composed of accumulations of coral skeletons that are poorly cemented internally. Dead branches of coral plates have interstices where small sclerosponges are common. Smith (MPRL, 1972) reported that an explosive blast on a lagoon pinnacle west of Jedrol "exposed unconsolidated to poorly consolidated coral material more or less in growth position." Sclerosponges, one of the prominent inhabitants of the unlighted holes in the reef, were abundant.

The sediment in these lagoon rim areas is not necessarily stable. At some coral patches, the sediment is scoured away at the base of the patch reef. Likewise, in

Fig. 9 Environments of lagoon margin patch reefs. Upper left: Coarse carbonate sand bottom with *Halimeda* spp. and other macroalgae, depth 6 m, near Choptop Reef. Upper right: Sediment/rubble bar near Choptop Reef produced by cross reef "rip." Lower left: "Satellite Reef" near Choptop Reef, comprised of a single colony of *Porites cylindrica*, probably torn from the main reef by storms. Several other satellite reefs are visible in the background. Depth on the bottom is 6 m. Lower right: Small patch reefs on the lagoon margin. A large cable from the atomic testing period is draped over a small patch reef (indicating an age of at least 20 to 30 years) with a colony of *Porites edouxyi* which has grown on the cable, depth 5 m.

some areas sand can be piled against the reef-killing corals or other sessile invertebrates. Coral colonies with half their surface buried and dead and the upper half healthy can be found at the point of reef-sediment contact on some patch reefs. Alteration of normal tradewind sea conditions can radically alter shallow water sediment distributions. Beaches grow or recede, islands change, and shallow sand bars on the lagoon margin appear or vanish with changes produced by passage of cyclonic storms (Nolan, 1975). It is not necessary for storms to pass close to Enewetak because the swell produced by a distant storm can accomplish the listed changes without high winds.

Lagoon Margin Zonation

The area immediately lagoonward of the reef flat is quite variable and of considerable biological interest. Various authors have described this zone, usually in combination with a description of a cross-reef flat transect.

Odum and Odum (1955) described the zonation of the interisland reef about 400 m north of Japtan Island. In many respects this is typical of windward interisland reefs of the central and southeastern portions of Enewetak. They described six zones from ocean reef to lagoon (a distance of about 450 m). These were (1) a buttress zone, (2) the algal-ridge, (3) an encrusting zone, (4) a zone of small coral heads, (5) a zone of small patch reefs "larger heads," and (6) a sand and shingle zone. Typical views of the bottom on the Odum and Odum (1955) transect are shown in Figs. 10 and 11. They make the point that the interisland reefs generally had more "vigorous" communities as opposed to reefs seaward of islands ("island reefs") where living corals were limited to the outmost portions of the reef. They believed this was due largely to different

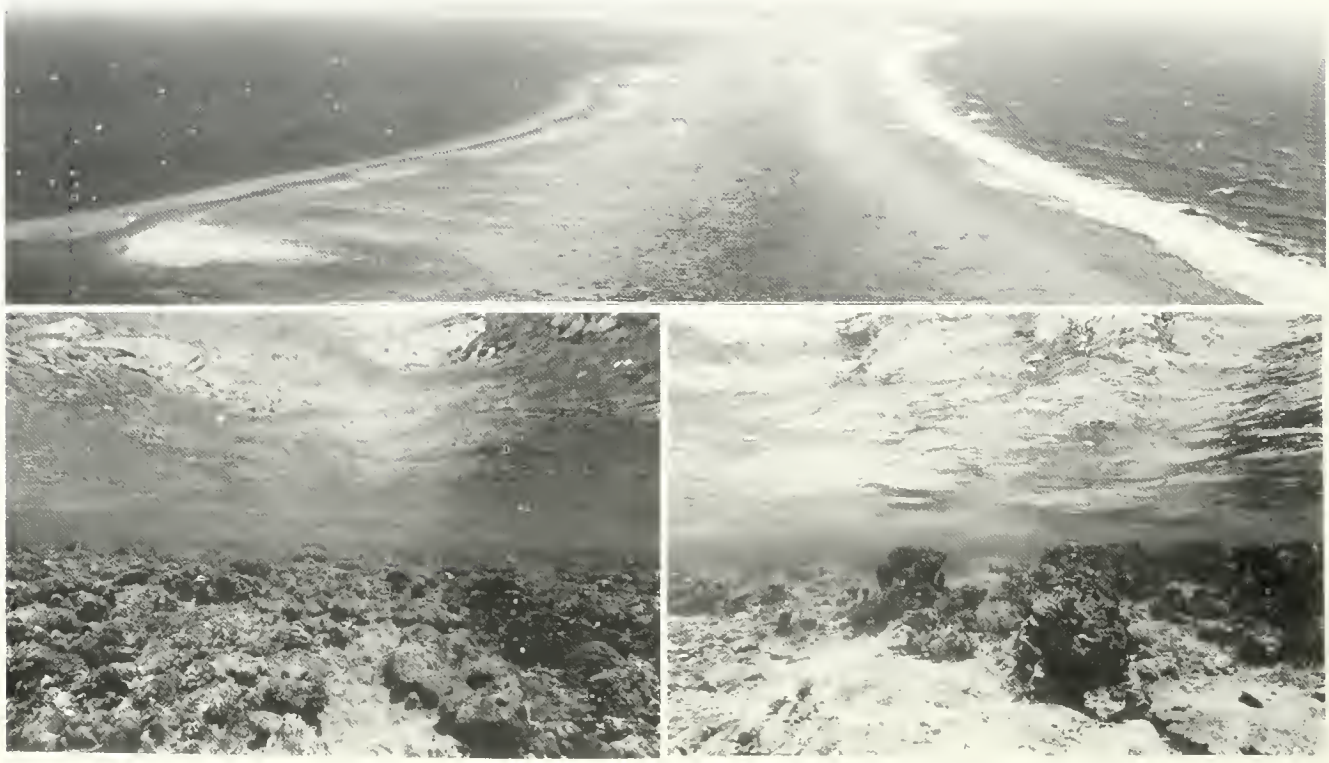

Fig. 10 Upper: Aerial view of the windward reef in the area of the Odum and Odum (1955) transect north of Japtan Island. The ocean is to the right and the lagoon to the left. The reef flat and associated reefs lie in the middle of the photograph. The photograph was taken while flying over the island of Japtan; Chinimi Island is visible with Ananij Island behind it. A normal surf is breaking on the windward reef with the lagoon margin very calm. Lower left: View of the zone of small coral heads on the Odum and Odum transect, depth approximately 1 m. Lower right: Junction of large coral head zone with the sand shingle zone of the Odum and Odum transect.

water circulation patterns. Johannes and Gerber (1974) illustrated a simplified cross section of reef near the transect of Odum and Odum (1955).

In the Odum and Odum (1955) study area, the bottom slopes gradually lagoonward from the encrusting zone. Individual coral colonies grow upward to a level limited by low water. In some corals the central portion of the colonies are dead with the sides continuing to thrive, producing structures known as "microatolls" (Fig. 12). These have been examined further on Enewetak reefs by Highsmith (1979) and will be commented on later. Often a distinct lagoonward edge to the reef flat pavement exists, and in many places, water flowing across the reef flat has eroded away and undercut the sediment beneath this lagoonward edge (Fig. 12). This has caused the reef flat pavement to collapse or buckle in places. This is most evident in areas where reef flat rips pass the edge of the pavement. The swift currents combined with the effects of dropping off the pavement have scoured deep potholes (as deep as 4 to 5 m) down into the sediments. The pavement is usually undercut on these edges.

The shallow reefs of the northern lagoon are poorly known. From Engebi west to Bokoluo, the reef is broad, as much as 1 to 1.5 km across, unlike southern reefs. Its zonation can be seen in aerial photographs but has not been investigated in detail. There is a reef flat about 100 m wide, then a broad (to 1 km) shallow area with coral heads. This coral head area on the west side of Engebi was examined. There were large microatolls of *Porites lutea* and acroporid corals on a level sandy bottom.

To the west of Bokoluo lies the open expanse of the northwest reef tract. It runs fairly straight to the northwest corner of the atoll at the West Spit. The gentle arc of the northwest reef is about 1.5 to 1.7 km across from the ocean to the deepening lagoon. From aerial photographs there appear to be four major zones: (1) a reef flat, (2) a coral head zone, (3) a clustered coral head zone, and (4) a patch reef zone. The reef flat is estimated to be about 150 m across, merging with a deeper coral head zone toward the lagoon. The coral head zone appears about 800 m across and is complex, with three visible components to it. The middle one-third of the coral head zone appears deepest, whereas the lagoonward one-third appears shallow. The density of coral heads in this area is high. Density data from photographs indicate there are at least 500,000 coral heads in this "coral head zone" between Bokoluo and the West Spit. There is scarcely any open sand of more than a few tens of meters between any

Fig. 11 Views of the sand-shingle zone of the Odum and Odum (1955) transect at Enewetak Atoll. Upper left: Coarse carbonate rubble and sand immediately behind the large coral head zone (depth 1.5 m). Upper right: General view of rubble area behind the large coral zone. Lower left: Carbonate sand farther lagoonward from the large coral head zone, depth 3 m. Lower right: Break in slope of sand-shingle zone where the slope increases considerably (to the right) toward the deep lagoon.

of them. From aerial photographs it appears many of the coral heads are arranged in a serial fashion across the reef with large numbers of them resembling striations across the bottom.

The clustered coral head zone is about 600 m across and has a lower density of coral heads than the previous zone. Those present are grouped together somewhat. Finally there is a zone of large patch reefs about 400 m wide. These patch reefs appear comparable in size to the larger patch reefs of the windward lagoon margin.

Channels Between Northern Islands

The channels between the closely spaced northern islands are of special beauty and biological interest. They are not true passes from ocean to lagoon because they draw their flow from the shallow reef flats to seaward but channelize the flow of water off the reef flat between islands. Viewed from the air, their bottom features show strong orientation to the current which funnels between the islands from ocean to lagoon, with reefs often elongated with the current and sediment washed out between patch reefs. These "passes" have a reef flat on their seaward end, but the cross-reef flat flow from an area of reef front several times broader than the channel is funneled into each one. The channels are often deep, but where current flow slows on their lagoonward end, they usually have a shallow, delta-like bottom.

A good example of a northern island channel is that between Lojwa and Aomen. At very low tides water flow across the reef flat is completely eliminated, with no current in the channel. At high tides with strong waves pumping, the current is swift, sufficient to deeply churn sediment from around patch reefs in the channel. The gaps between reefs have the sediment scoured away, appearing darker blue when viewed from above, whereas areas on the sheltered, downcurrent side of the patch reef have

Fig. 12 Upper left: Microatolls *(Porites lobata)* at the north end of Chinimi Island, Enewetak. At low tide the water is essentially at the upper level of the microatolls. Secondary growth is also occurring in the central area of the top of the microatolls. Upper right: Aerial view of lagoonward edge of the reef flat showing erosion at the end of the reef pavement caused by water flowing across the reef flat. Lower left: Typical views of patch reefs in the Lojwa-Aomon interisland channel. Extensive sculpturing of the sediment bottom is caused by currents which course through this channel at high tide. Lower right: Area of the Lojwa-Aomon channel with sand built up behind (down current side of) a large patch reef.

white sand built up. The width of these "tails" of sediment decreases downcurrent of the reef. The upcurrent sides of the patch reefs have the sand washed away to depths equal to those on the sides of the reef. Corals and benthic invertebrates are usually well developed on the upcurrent end and sides of reefs.

The deepest portions of the channel are 6 to 7 m, and some patch reefs are emergent at low tide (Fig. 12). The reefs in this channel have changed little in the last 32 years based on aerial photographs taken in 1949 and 1981. The major patch reefs are identifiable, but some of the lagoonward patch reefs seem to have been somewhat buried by sediment.

Other interisland channels are similar. Rock surfaces are heavily grazed by herbivorous fishes. Small caves and overhangs off the patch reefs are lined with encrusting coralline algae. These patch reefs are one of the few places within the lagoon where branching coralline algae are found. Sediments are coarse, with predominantly large foram tests, coral, and *Halimeda* bits. The reefs of the channel between Lojwa and Alembel seem to have been devastated by a storm during the last decade. Very little live coral and few benthic invertebrates are on them. Allen (1972) used this channel as a primary study site for his anemonefish work. One patch reef in the channel had more than 75 clusters of 10 to 30 individuals of *Physobrachia douglasi*, with larger numbers of *Amphiprion melanopus*, in an area of only 700 m^2. In the summer of 1981, this area was re-examined for anemones and *Amphiprion*; no anemones or anemonefishes of any type were found.

In channels farther north, corals and other invertebrates seem healthy. Some of the channels were noted for their abundance of large tridacnid clams, but many of these clams have been eliminated since the repatriation of the Enewetak people.

Passes

There are three passes from ocean to lagoon with sufficient water depth for boats to regularly traverse them. They are the "deep passage" (east) between Medren and Japtan, the "wide passage" (south) between Enewetak and Igurin, and the "southwest passage" between Kidrenen (south) and Biken. Various details of these passes have been discussed in Chapter 3, this volume.

The biological communities of the deep channel and its margins have not been well described. Hobson and Chess (1978) discussed the patch reefs and plankton communities in the area between Japtan and Jedrol Islands which are affected by currents coursing through the deep channel, but their study site was not in the deep channel proper.

The northern side of the deep channel slopes steeply from depths of only a few meters. To the east of Jedrol there is actually a "barrier" reef awash at low water which is constantly exposed to oceanic swells entering the lagoon through the deep channel. The northern slope of the deep channel to depths of 30 to 40 m is a nearly 45° angle rocky slope with abundant corals and reef-associated invertebrates. At depths of 25 to 40 m, the bottom levels and the central portions of the channel are probably relatively flat. There is a downslope sediment transport along this face, and below 30 m where the bottom begins to level, sediments also begin to dominate the bottom compared to exposed rock outcrops.

The easternmost extension of the shallow wedge where the channel splits is distinct, the "cutting edge" being only a few meters wide and descending at about a 45° angle from 6 m to depths below 30 m. The coral communities of the shallow reef and slope are rich. The fish communities of the north side of the channel are diverse and abundant with zooplanktivores more dominant than in other areas.

The south side of the deep channel is different from the north, with the bottom sloping gradually as a sediment slope with little or no exposed rocky substratum. A shelf between 30 and 36 m in depth extends a kilometer or more northwest from Medren into the lagoon.

Little is known about the area of the wide channel. Aerial photographs show large patch reefs on a sandy bottom scattered across the entire 9.3 km width. The crest and outer slope of the sill was examined about 1.6 km west of Enewetak and had large, rocky patch reefs, not unlike large lagoon margin patch reefs at 18 to 20 m depth (Fig. 13). The patch reefs had relatively little live coral but had abundant *Halimeda* spp. and *Asparagopsis taxiformis*. The most common corals were *Pocillopora* spp. The sediment was coarse, dominated by *Halimeda*, with small ripples at 22 m depth. There were small rocks between the much larger reefs but little grew on them. To seaward, the sediment bottom sloped perceptively. At 30 m, it was nearly all sediments with only a few rock patches and sloped at an angle of about 15° (Fig. 13). Below that depth, the slope increased to about 20° at 40 m and more with increasing depth.

The southeast passage consists of sandy channels between elevated fingers of reef for 6.5 km southeast of Biken. Atkinson et al. (1981) estimated the cross-sectional area of the southwest passage as only 26% of the deep passage and 6% of the wide passage with no net inflow or outflow. The reef fingers have well-developed coral communities which do not differ greatly from the interisland

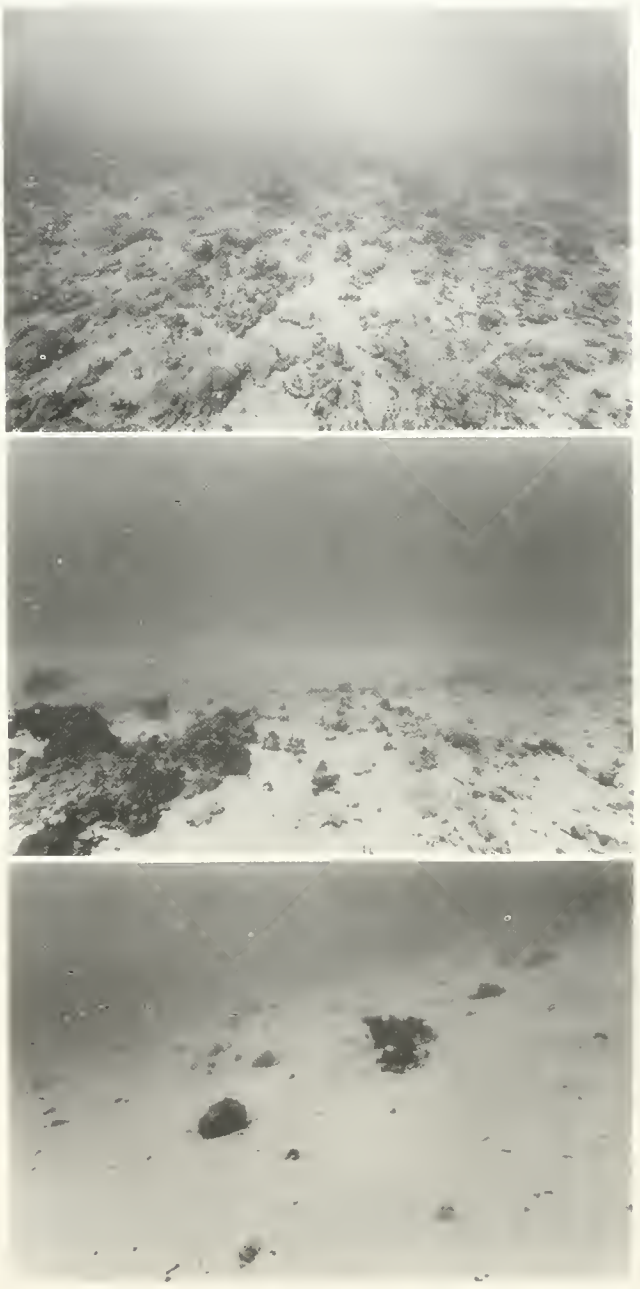

Fig. 13 Views of the bottom, wide (south) passage, Enewetak Atoll. Upper: Rubble substratum at about 20 m depth looking downslope. Middle: Juncture of rubble and sand substratum at 30 m depth, looking downslope. Lower: Sand slope substratum with isolated coral boulders at 40 m depth. There is considerable evidence of downslope transport of sediment in this view.

patch reefs on the windward side. The sand channels shoal gradually from the lagoon to their shallowest point, then again gradually deepen to seaward. Near the precipitous reef edge to seaward, the channels quickly steepen, then plunge down the near vertical slope. Sediment is transported over the drop-off here with heavy scouring of the reef face below the sand chutes.

Algal Ridge

Before considering the true seaward reefs, it is worthwhile to mention the zone marginal to the reef flat. This is the "algal ridge" which is truly intertidal but has extreme relevance to subtidal seaward areas.

The seaward reef on the windward side of Enewetak is mostly devoid of live coralline algal ridges. Live algal ridge (often termed "*Lithothamnion* ridge" by earlier authors) occurs only along one section of windward reef about 200 m in length at Ananij Island. This section is readily distinguished by its pink coloration, produced by the abundance of *Porolithon* species, as compared to the dull surface of the algal ridge dominated by macroalgae.

Three species of *Porolithon*, as identified by Lee (1967), have been found on the Ananij algal ridge. Large portions of the surfaces of the spurs are covered with crustose corallines, probably *Porolithon onkodes*. Distinct colonies of *Porolithon craspedium*, often with blunt fingers forming a lobate mass, occur scattered on the upper surface of the spur. *Porolithon gardineri* seems the least common species, although its colonies are often irregular masses 20 cm or more across. It appears limited to the sides of the spurs, not being found on the upper surface among *P. craspedium*. Within the sponge-like structure of the spurs at Ananij, virtually all visible internal surfaces are covered by coralline algae, but the species involved are not known.

Inshore from the live algal ridge at Ananij is a slight depression of the reef flat where colonies of *Acropora* sp. flourish. Small patch reefs occur on the hard pavement here which has water on it even at low tides. The *Acropora* sp. colonies are emergent at low tides. The small coralline algae *Neogoniolithon rutescens* is occasionally found among these patch reefs but not on the more exposed spur and groove areas.

Seaward Reefs

Smith and Harrison (1977) described the windward reef slope off Chinimi Island, and since their study other areas have been examined. The spurs are relatively flat on top and occasionally have undercut, overhanging edges (Fig. 14). Algae and invertebrates are abundant on the sides of these spurs. Sea urchins have eroded elongate grooves in the rocks on the sides of the spurs which afford protection from wave action and predatory fishes (Fig. 15).

The bases of the grooves are floored with boulders and cobbles, precluding any significant benthic invertebrate populations (Fig. 14). The walls of the grooves, however, have on them small corals and invertebrates adapted to withstand the wave surge. On the upper surfaces of the spurs, small corals grow with an abundant film of algae on rock surfaces (Fig. 14).

Smith (MPRL, 1972) dissected a spur and groove system north of Japtan using explosives. "The spur proved to be dense, well-cemented coral rubbles covered by a veneer of live encrusting coralline algae." He felt that, except for relatively minor growth by the coralline algae, the spur and groove systems are erosional features.

On windward reefs the spur and groove zone and the area immediately seaward of it are areas of very high fish abundance (Fig. 15). Herbivorous parrot fishes and surgeonfishes feed in this productive area and range on to the algal ridge and reef flat from there. At low tide these shallower areas are dry, requiring their exploiting fish populations to move elsewhere.

The spur and groove zone seaward of the areas of *Porolithon* algal ridge at Ananij is different from other areas examined where the ridge is "dead." The cover of benthic invertebrates appears higher there. This is the only area on the windward shore where the club-spined urchin *Heterocentrodus trigonarius* is known to be abundant, both in holes on the sides of the spurs and on the algal ridge. A form of branched *Acropora* sp. coral with other corals and *Halimeda* sp. algae with distinct laminations occurs there. This form of *Acropora* has not been seen elsewhere (Fig. 15).

Off the north end of Enewetak Island, the sides of the spurs are lined with grazed macroalgae and occasional patches of coralline algae. The rock-boring urchin, *Echinometra methaei*, is abundant in grooves in the sides of the spurs. In small caves and on overhangs a wide variety of benthic invertebrates occurs.

On the sides of the spurs' upper surface are small head corals and soft corals. There is less coral on the tops of the spurs, and the area is more dominated by macroalgae. At the seaward end of the spur, colonies of stony corals, *Heliopora caerulea*, and soft corals are common. These are larger than those of the top or sides of the spur. Some sizeable encrusting sponges may also occur in this area.

Several herbivorous fishes are characteristic of this spur and groove zone. The surgeonfishes, *Acanthurus achilles*, *A. guttatus*, *A. triostegus*, and especially *A. lineatus* are generally found in any abundance only in this area on the windward shore. One small damselfish, *Plectroglyphidodon phoenixensis*, is common on the windward shore and occurs only in the spur and groove area.

Seaward of the spur and groove, the rocky bottom levels somewhat with only a slight seaward slope (Fig. 14). The bottom often has minor undulations of its surface, occasionally with small shallow grooves oriented perpendicular to the reef front, but generally it has few distinguishing features. The irregular pits and grooves of rock-boring sea urchins, *Echinometra mathaei*, and lesser numbers of some diademnid urchins (Fig. 16) are often abundant. A few small- to medium-sized corals occasionally occur on this "barren" zone (Fig. 15). Viewed from the air, this zone

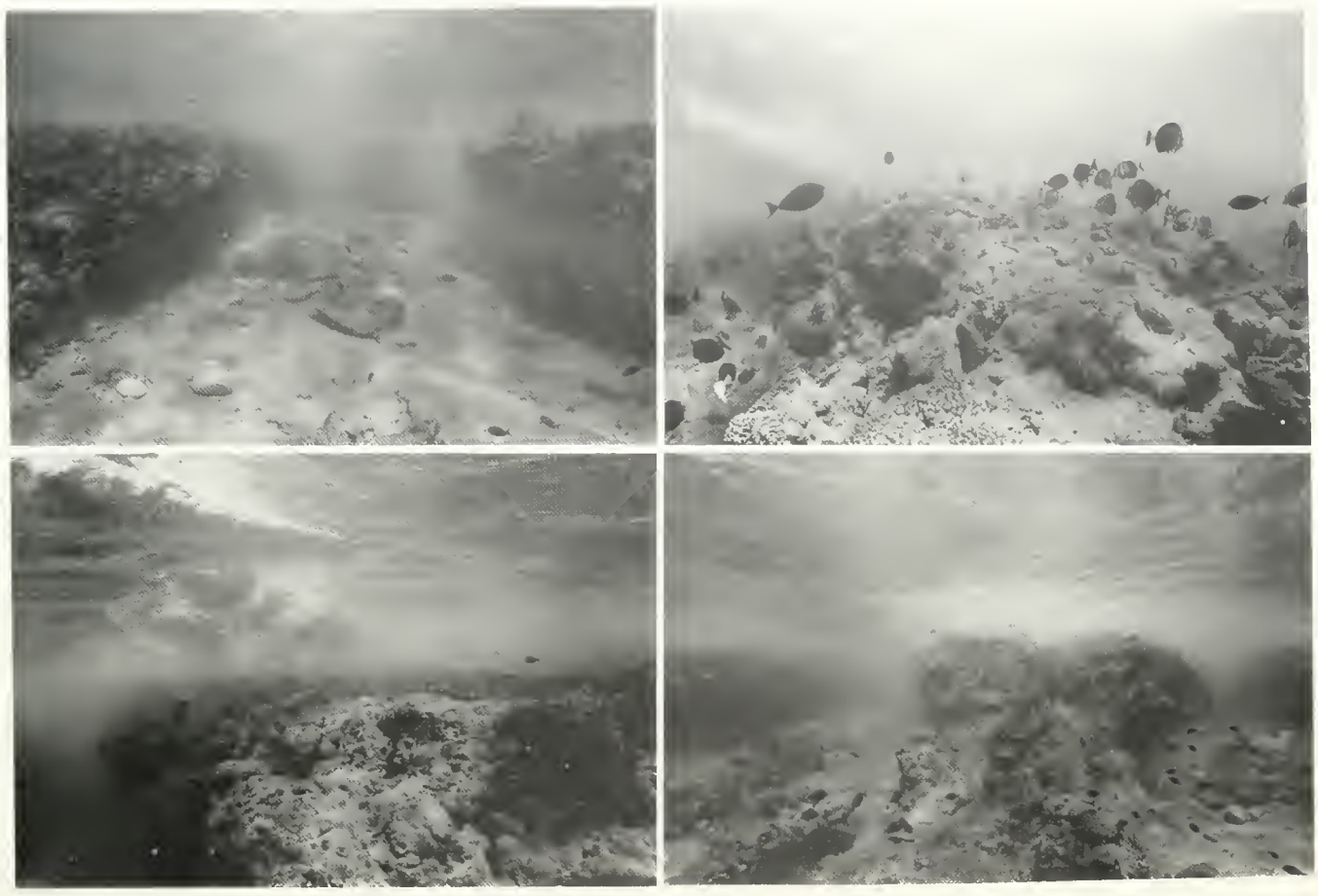

Fig. 14 Typical views of the spur and groove zone off Enewetak Island. Upper left: Shallow groove with large coral boulders in its center which are set in motion during periods of high waves. These effectively keep the grooves free of sessile benthic macroorganisms. Upper right: A variety of herbivorous fishes at seaward end of a spur. Lower left: Spur seaward of the Enewetak Island reef flat with breakers rolling over it. Lower right: Seaward end of a spur with a breaker forming at its prow. The shallower water depth on the spurs causes waves to break there sooner than over the grooves.

appears to be a uniform light color. The rock shelf width varies around the atoll. Off Enewetak Island it is relatively wide, about 200 to 300 m, but farther north it becomes narrower, probably less than 100 m wide.

The rock surface of the shelf often has evidence of extensive boring by clionid sponges. Large areas of substrate may have the tiny, dark oscula visible, but these are not apparent on superficial examination (Fig. 16).

Smith and Harrison (1977) have described a windward reef slope from off Jinimi Island in connection with estimates of calcium carbonate production there. The reef crest had essentially no corals. Moving seaward from the reef crest and spur and groove zone, the bottom slopes gradually from 4 to 5 m depth to about 8 m and is essentially a rocky pavement with minor surface undulations. Smith and Harrison (1977) estimated only 10% coral coverage in their study area at 7 m depth. Seaward, the amount of coral cover increased with depth, although the slope may increase only slightly with 15, 20, and 25% at 11, 15, and 21 m depth, respectively. At 50 m, coral coverage was virtually zero. Smith and Harrison (1977) found that the vasiform *Acropora cythera* was the most conspicuous coral in their study area, with its nearly flat upper surface well adapted for capturing sunlight. They performed coral and coralline algae incubations using clear acrylic domes, where possible, at depths to 21 m. Steadily decreasing rates of calcification with increasing depth were found. Overall they believed the seaward slope of windward reefs at Enewetak (the "mare incognition" of Ladd, 1961) has only a small role in the $CaCO_3$ mass balance of the atoll.

Large numbers of vasiform *Acropora cythera* colonies, up to 2 m in diameter, were found by Smith and Harrison (1977) at 15 to 25 m at their study area (Fig. 1A of that paper). Colonies had a maximum of 13 growth bands (annual), and they considered that the major typhoon in late 1962 (their observations were in late 1976) may have devastated *Acropora* corals in that area. Smith and

Fig. 15 Upper left: Larger shoal of *Acanthurus triostegus* in the spur and groove zone, Ananij Island, depth 4 m. Upper right: Unusual growth form of *Acropora* sp. found seaward of the area of live algal ridge, Ananij Island, Enewetak Atoll. Lower left: Grooves eroded in the side of spurs by sea urchin *Echinometra mathoei*, windward reefs, Enewetak Atoll. Lower right: Isolated coral head located to seaward of the spur and groove zone, windward shore of Enewetak Island, depth 7 m.

Harrison's (1977) study area was disrupted by a severe typhoon in January 1979 (Alice) in which all the large *Acropora* colonies at 15 to 25 m were reduced to rubble (Fig. 16), confirming their suspicion that typhoon-strength storms are capable of such disruption to depths near 20 to 25 m.

The outer slope or "drop-off" begins at depths of 18 to 23 m as a distinct change, from a gentle slope of a few degrees to an angle of approximately 30° to 45°. This slope rapidly increases with depth (Fig. 17). The deep reefs of the windward side have been severely damaged by storms so that there is relatively little live coral and tremendous amounts of rubble at 15 to 30 m depth (Fig. 16). Along Enewetak Island to Medren, there is generally a sandy zone at 30 to 40 m which appears as an irregular light band from the air. Below this depth sand channels alternating with reef can be seen on the outer slope when viewed from the air; this sandy zone is not apparent from the air on reefs of the islands farther north.

Vosburgh (1977) experimentally determined that waves of near 5 m height did not produce sufficient water motion at depths of 9 to 21 m to cause breakage of the skeleton of large, healthy *Acropora cythera*. He reported that although this species is found at less than 2 m depth in sheltered areas of the lagoon, it occurs commonly on the windward reefs only at depths below 8 to 10 m. Sheltered lagoon colonies were generally larger than those on the windward reef, and depth distribution and colony size are related to wave exposure. Although his estimates of near 5 m waves are based on the highest 1% of waves observed during the windiest portion of the year, he points out that typhoon waves, not considered in his study, "might cause catastrophic breakage over the entire species range on the (windward) terrace."

The steady seaward slope of the windward reef generally prevents accumulation of large amounts of sedimentary material. At the slope break at about 18 to 20 m depth, some sediment-bottomed channels occur which can

Fig. 16 Upper: Carbonate rock substratum heavily bored by the sponge *Cliona* sp. on the windward reef, Enewetak Island, depth 8 m. The dark oscula of the sponges are visible over much of the substratum, although the tissue of the sponge is located internally beneath the surface of the rock. Middle: The area of the shelf edge break (20 m depth) off Enewetak Island. There is very little live coral in this area with only a single table *Acropora* visible among large amounts of coral rubble. Lower: Outer slope at 25 m depth, Enewetak Island, coral rubble going down the slope into deeper water.

serve to transport sediment into deeper water. Below the shelf break, larger amounts of sediment are visible on relatively horizontal areas, but the slope limits the amount of build up.

The reefs of the leeward side have extremely steep slopes. The distance between the reef crest and the steep slope into deep water changes with location. Along the southwestern islands (Ikurin through Kidrenen) there is a narrow shelf sloping gently from about 3 to 15 to 18 m. This shelf is generally about 100 to 150 m wide and has a well-developed coral community on the rocky shelf. Most of the corals are small, less than 10 years old, implying recent devastation, probably by storm waves. Sand channels occur perpendicular to the reef front which is at the head of reentrants on the reef face. The change to a steep slope occurs at about 15 m where it becomes a 45° to 60° slope to the limit of scuba diving. A typical profile of a southwest island reef is shown in Fig. 17.

To the west of Kidrenen, the reef remains unbroken until the southwest passage. The bottom slopes gently, then progressively becomes steeper with virtually no shelf to a near-vertical face at about 10 m depth. The horizontal distance from water a few meters deep to the vertical face is less than 50 m. This extremely steep profile is even more pronounced on the reef north of Biken to the West Spit. Reentrants penetrate the reef face with *Halimeda* dominated sediments on shelves on a steep slope into the deep water (Fig. 17).

The leeward reef crest near the island of Ikuren has a healthy cover of coralline algae on its upper surface, even though on the leeward side of the atoll, small to moderate surf usually occurs, which is produced by the long, low swell from the west. Large numbers of herbivorous fishes occur here, essentially the same species as are found on the windward spur and groove areas. The two areas are similar; but near the southwest islands the grooves, strength of surf, and various invertebrates are lesser developed. Seaward of the reef flat are often small high relief rocky structures with flattened tops and abundant coral (Fig. 18). Species of *Acropora*, *Pocillopora*, and *Heliopora* are common on the edges of the coralline flat. The cidaroid sea urchin, *Heterocentrotus trigonarius*, is found deep in small caves and crevices of the outlying rock structures among coralline-covered fossil coral branches. Around and to seaward of these structures is often a bottom at 5 m depth composed of large coral boulders and shingle. Much of the hard substrate in this area not covered by hard or soft corals has coralline algae growing on it. These algae often have large numbers of grazing marks almost certainly from parrot fish (Fig. 18). The alga, *Asparagopsis taxiformis*, is extremely abundant; its upright tufts in evidence on nearly all rocky surfaces (Figs. 19 and 20).

A rock substrate begins within 20 to 40 m of the reef flat with occasional large vertical knobs of rock covered with hard and soft corals. Urchin grooves are evident in the rock, but diademnid urchins were seen much more often in them than *Echinometra mathaei*.

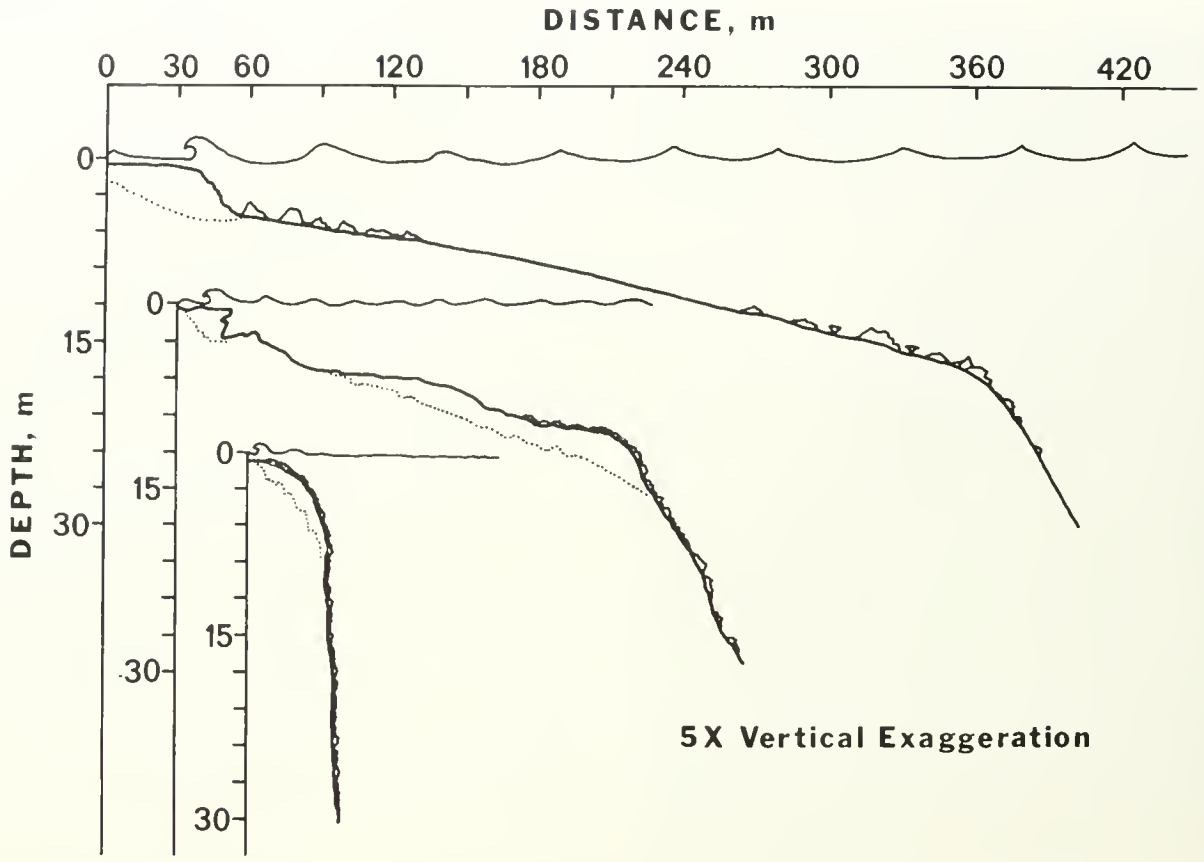

Fig. 17 Typical slope profiles of Enewetak Atoll seaward reefs. The profiles, which are vertically exaggerated, are from a windward reef off Enewetak Island (upper), a leeward reef off Ikuren (southwest islands) (middle), and a leeward reef north of Biken (lower). Dotted lines represent the bottom in areas of sand channel reentrants of the reef face. Waves shown on the surface reflect the normal wave conditions on these different areas.

The rocky shelf slopes gradually seaward, and at about 8 to 10 m depth sand channels begin to appear on its surface. There is considerable relief between the reef fingers at about 9 to 10 m and the channels at 12 to 14 m (Figs. 19 and 20). The sides of many of the fingers are nearly vertical and often undercut. These overhanging walls have dense coverage of coralline algae and abundant *Halimeda*. The sediment in the channels is coarse, derived largely from *Halimeda* flakes and often has wave ripples on its surface from the long period swells. The upper portions of the reef fingers have dense coral on their tops and sides. Coral coverage at 12 m depth on the top of the fingers at the shelf break is 80 to 90% in some areas. A few large head corals occur but most are small to medium acroporids. They are at most 25 to 40 cm across and probably reflect recruits after storm destruction of most of the previous acroporids (Fig. 19).

The bottom slopes away at the shelf break (12 to 15 m) at a 45 to 60° angle. Most of the sand channels continue down the slope as sediment chutes into deep water. These chutes are cut back into the reef face and have sediment down them to the limit of visibility (Fig. 20). Adjacent rock surfaces have abundant corals, the same types of species that occur in shallower water. Live *Halimeda* is abundant all down the slope to over 60 m.

Hillis-Colinvaux (1980) found four species of *Halimeda* on the seaward reef off Mut at 10 to 15 m depth. She estimated cover of *Halimeda* on this bottom as about 15% and commented that *Halimeda* was much more conspicuous on the spur reef structure than she would have expected on a reef buttress in Jamaica.

Halimeda flakes dominate the sediments of all leeward side oceanic reefs. Below about 20 m depth, sediment builds up on any nearly horizontal surface, particularly near the reentrants which are the primary "down chutes" for sediment.

There are many overhangs and small caves formed by coral plates on the leeward reefs. Incredibly delicate large colonies of stylasterine corals grow in their dim recesses. Three species of sclerosponges—*Astrosclera willeyana*, *Acanthochaetetes wellsi*, and one unidentified species (Basile et al., 1984)—are found in caves along the reef

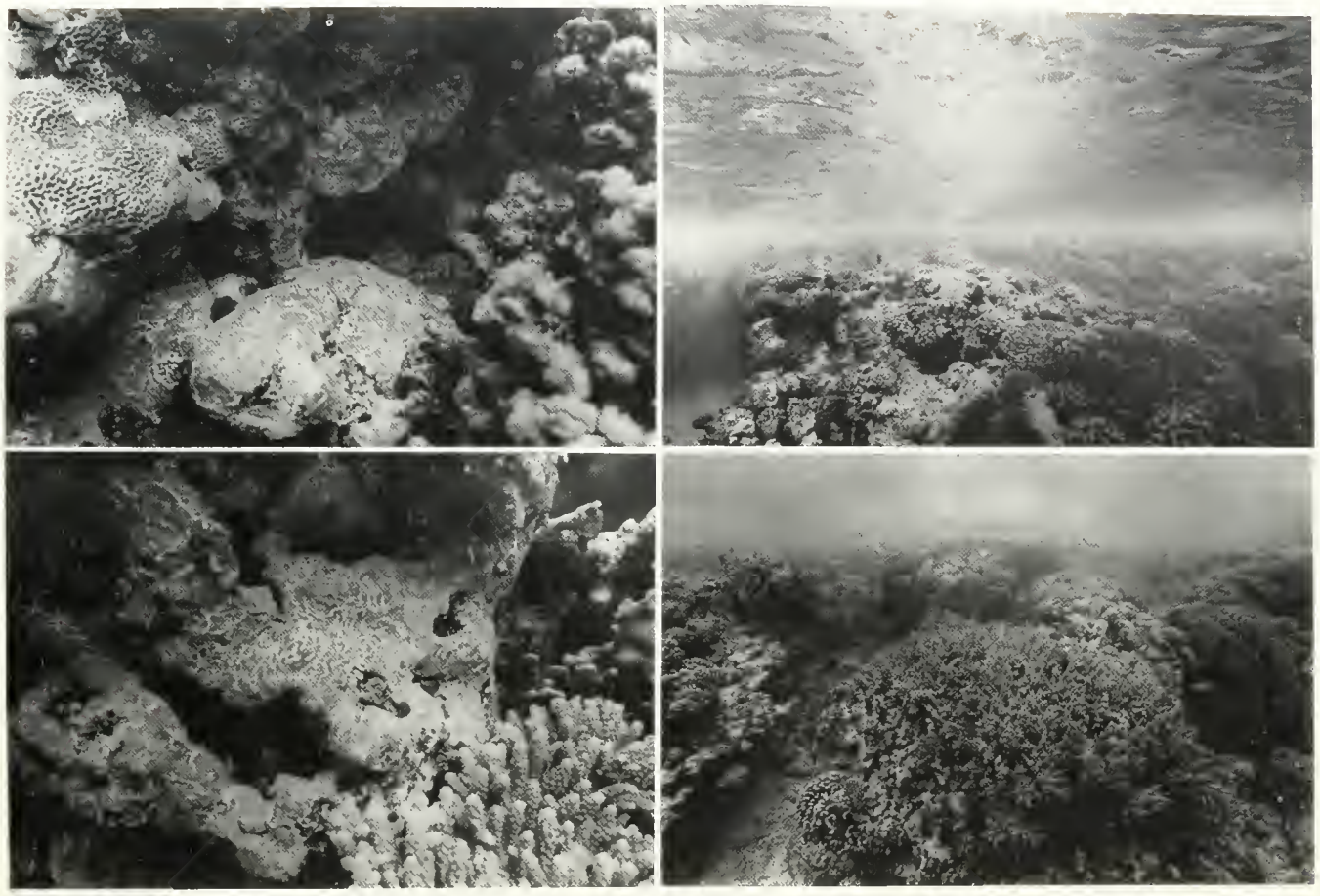

Fig. 18 Typical views of seaward reefs off the southwestern islands, leeward side of Enewetak. Upper left: Area of heavy grazing, probably by parrot fishes, on rock substrata. Upper right: Seaward end of the reef flat with short "grooves" going into the reef flat. Lower left: Heavily grazed substrata, with parrot fish tooth marks, depth 2 m. Lower right: Seaward end of the reef flat with some large coral colonies.

face, but they are small and do not produce significant amounts of calcium carbonate.

There are many large fan-like gorgonians along the vertical face, in addition to widely scattered colonies of antipatharians (black coral). Large black coral "trees" are rare in these (and all other) areas.

On the leeward side of Enewetak Atoll there is an algal ridge-type structure which is not well known. Marsh (1970) reported one area at Igurin to have "a relatively good growth" of coralline algae. The leeward ridge is in many places slightly submerged at low tides, but never as emergent as the windward reef flat.

The outer slope of Enewetak below scuba diving depths was examined to a depth of 365 m with the research submersible *Makali'i* during the summer of 1981. Twenty-two dives were made on the seaward face from Biken around the southern end of the atoll to south of Runit (Colin et al., 1986). The seaward reefs of the northern half of the atoll were not examined.

The depth profiles of five areas on the seaward margin are shown in Fig. 21. The profile of the outer slope of Enewetak is very steep, an angle of about 60° between 90 and 360 m with the leeward slope being slightly steeper. Emery et al. (1954) and subsequent writers have commented on the steep slopes of atolls in the northern Marshalls. Their opinions were based on echo soundings and were confirmed by observations from the submersible *Makali'i*.

To depths of about 300 m the slope is generally rock with small accumulations of sediment. Every near-horizontal surface has a dusting of sediment, and small ledges have accumulations varying with the area where sediment can rest. There is little significant accumulation of talus to depths of 200 to 300 m from upper areas as the slope remains steep enough to prevent talus accumulation. Incised, highly polished vertical grooves occur in the rock face serving for downslope transport of sediment. At depths between 200 and 300 m, large talus begins to occur in the form of broken colonies of coral and reef plate brought down the slope. In some locations a *Halimeda* sediment-dominated slope began at about 270 to 300 m depth with a slight decrease in slope. Along with this were

Fig. 19 Typical views of seaward reefs off the southwestern islands off Enewetak. Upper left: Rubble area to seaward of the reef flat, depth 5 m. Upper right: Area of isolated coral heads seaward of rubble area. Lower left: Small acroporid corals on the outer reef face, southwestern islands, depth 20 m. These corals are probably less than 10 years old and may represent recruits after major storm damage to the community. Lower right: Outer slope along the southwest islands, depth 20 m. The bottom slopes away at about a 45° angle to great depths.

often mounds or ridges of talus and carbonate blocks more than 1 m across.

There was some relief on the rock face at 100 m to about 180 m, often with the surface pitted with shallow depressions less than 50 cm across. There were occasional small caves, seldom penetrating more than 1 m into the reef face.

Stony corals were observed to grow relatively deep. Below about 60 m only flattened forms were found. Sparse coral communities occurred to at least 90 m depth, with individual colonies occurring to slightly more than 100 m depth. Similarly, attached and living *Halimeda* colonies were found at more than 120 m (Hillis-Colinvaux, 1986). Green algae were found to almost 150 m and coralline algae to nearly 200 m.

Some differences in biological zonation were noted between the windward and leeward slopes. The windward areas have more coral at 60 to 90 m depths, larger populations and diversity of small reef fishes from 60 to 200 m, and generally more benthic invertebrates.

In the wide channel area, there seemed to be much down slope transport of sediment, although again the steep slope at 100 to 200 m trapped relatively little sediment on the face. Below about 200 m, huge slopes of *Halimeda* with seapens growing on them were found (Colin et al., 1986). At the eastern edge of the wide channel this unconsolidated slope was alternating elevated areas of talus and the sand between "pure" sand slopes.

Lagoon Water Column

The waters of the lagoon have not received adequate attention. Recent work has examined the circulation of the lagoon (Atkinson et al., 1981), the relationship between reef-produced organic material and lagoon plankton (reviewed in Gerber and Marshall, 1982) and plankton

Fig. 20 Reentrants of the reef face, southwest islands, Enewetak Atoll. Upper left: Sand channel in between elevated reef fingers, depth on sand approximately 12 m. Upper right: upper portion of a reentrant on the outer slope at 30 m depth. Lower left and right: Sediment transport via reentrant down the outer reef face, southwestern islands, depth 40 m.

composition (Gerber, 1981), but these are only a bare beginning. The open lagoon is generally rough and less than ideal for working in a small boat. Navigation and positioning are difficult because the islands of the atoll rim are so low that in the center of the lagoon little land is visible.

Water column productivity within the lagoon has not been well documented. The author has seen, on several occasions, large blooms of phytoplankton in the northern and western lagoon. These were sharply differentiated areas of "brown water" many kilometers in length and, on two occasions, as surface slicks many centimeters thick. The surface slicks occurred under extremely calm conditions and were nearly linear masses of tan phytoplankton, tens of meters broad and over 1 km in length. Thickness was not determined but was believed to be at least 30 cm. The blooms may be associated with water of lengthy residence time in the lagoon since they have been observed only from areas where this is typically the case.

Dense swarms of zooplankton were often observed in the lagoon by scuba divers, often within a discrete portion of the water column. During the summer, particularly huge numbers of salps and ctenophores were observed many times on the reef. Gerber and Marshall (1982) documented a "bloom" of pteropods and a subsequent population decrease in the central lagoon during a 4-week period.

The unidirectional flow of water from windward reefs across the reef flat to the lagoon is significant not only in the physical flushing of the lagoon but as a mechanism by which increased nitrogen, produced by nitrogen fixation on the shallow reef flat (Webb et al., 1975), reaches the lagoon.

Webb et al. (1975) felt there were three important routes by which *Calothrix crustacea* fixed N_2 enters the remaining reef ecosystem. First, fish grazing and the low assimilation efficiency (Chartoch, 1972) of herbivorous fishes makes the fixed nitrogen available. Second, fragmentation of *Calothrix* and lagoon transport makes it available to herbivores and detritivores in the lagoon. Third, 40 to 60% of the nitrogen fixed is released in solution and is available for other organisms.

Gerber and Marshall (1974) have shown that detritus flowing off the shallow reefs forms a major component of

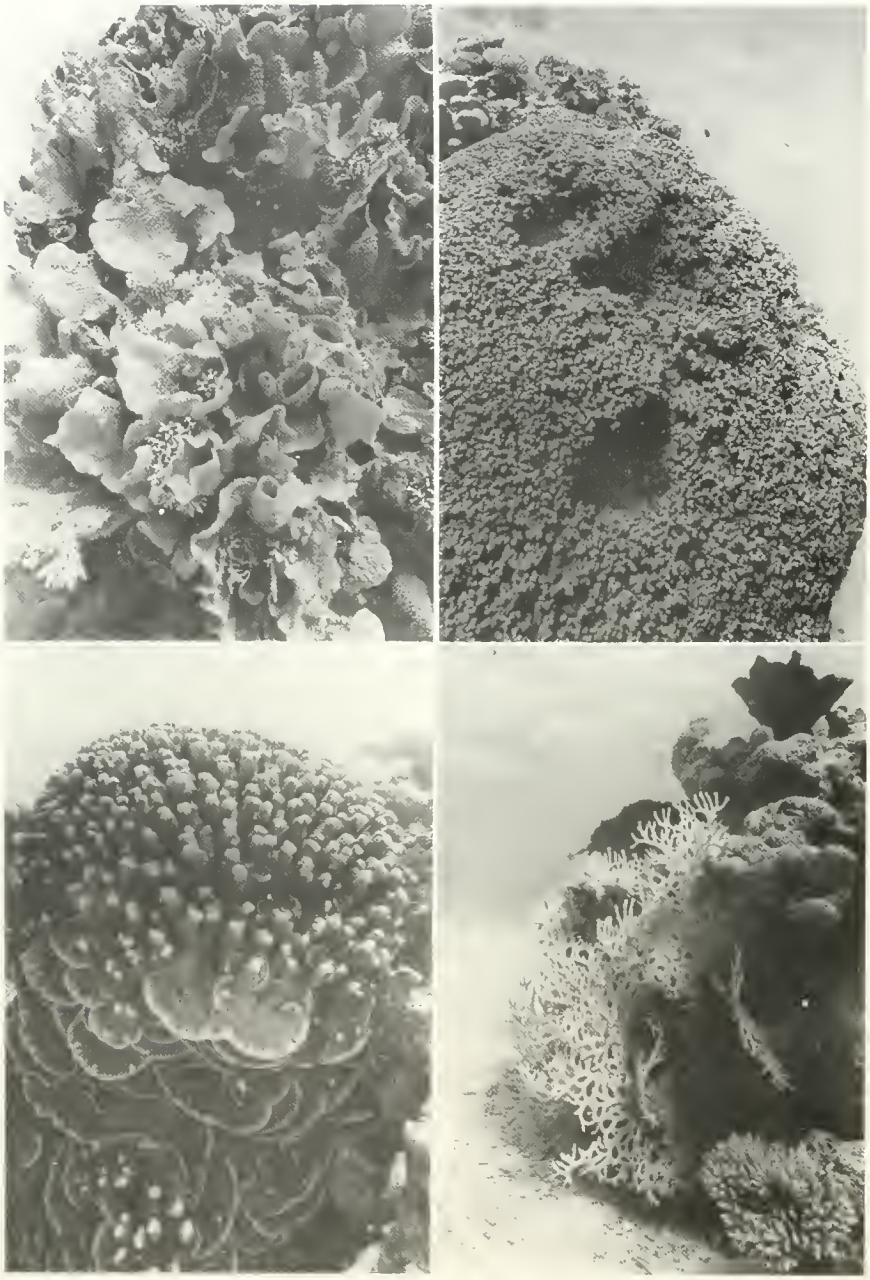

Fig. 21 Views of lagoon reef coral colonies. Upper left: *Turbinaria* sp. Upper right: Large colony of *Porites rus* with areas removed, possibly by coral damaging fishes. Lower left: *Porites rus*, large colony showing a shift from columnar to plate-like growth with depth and exposure to less light. Lower right: Fan-like growth form of the hydrozoan *Millepora* sp. on a lagoon margin.

ingested material in two abundant lagoon zooplankters. Furthermore, lagoon copepods have also been known to ingest and assimilate such particulate matter (Gerber and Gerber, 1979).

Gerber and Marshall (1982) suggest that the occurrence of planktonic organisms in the central lagoon results mostly from production and consumption in the water-column community. They indicate that the reef communities are the sources for a large percentage of the carbon and nitrogen fixed and present in lagoon waters. The phytoplankton community of the lagoon is also important as a food chain base, but the relative importance of each is not well understood.

Gerber (1981) documented the diversity and abundance of zooplankton at two stations in the lagoon. Ninety six species of copepods and species of chaetognaths, larva-

ceans, mysids, euphausiids, amphipods, siphonophores, pteropods, dinoflagellates, medusae, other planktonic crustacea and larval forms were found. One station, near the Enewetak–Medren reef flat had lower abundance, fewer species of typically planktonic organisms, and more meroplanktonic and benthic forms than the mid-lagoon station. There was considerable variation in densities of zooplankters among samples taken during the same study periods of a few to several weeks at the mid-lagoon station.

Gerber and Marshall (1982) reported that lagoon concentrations of copepods, pteropods, and larvaceans were higher during their summer sampling period. Phytoplankton biomass in mid-lagoon in summer was also about twice that of the winter. Individual components of the zooplankton changed their densities considerably during periods of several weeks during the summer. Copepods and larvaceans increased 1.5 to 3 times. Pteropods increased 20 times in 4 weeks, then declined rapidly.

Coles and Strathmann (1973) collected mucus flocs from the water column at Enewetak and other areas and found them to represent substantial quantities of organic matter when compared to particulate organic material in the water. They noted that under calm conditions few mucus flocs were seen in the water at Enewetak, but after a storm abundant large flocs were seen passing into the lagoon.

ASPECTS OF MARINE COMMUNITIES AT ENEWETAK

Reef Growth and Destruction

Coral reef growth is a balance of factors: the accretion of calcium carbonate by stony corals and other calcifying organisms in addition to the consolidation of these materials into a cohesive structure versus the erosive effects of grazing pressure, physical weakening, and destruction of the reef structure. Much work at Enewetak has focused on questions related to the growth and maintenance of reefs. Not all is summarized here but some environmental factors concerning reef growth are.

Calcification of corals and other organisms can be affected by environmental conditions, such as light, temperature, and water movement over the range of conditions under which the organism can survive. Stony corals are also known to "compete," albeit in a relatively slow manner. Methods include overgrowth, reducing the light necessary for calcification and growth of competitors, and by "extracoelentric digestion" in which mesentarial filaments are extended to "attack" and kill tissue of other species growing close by.

The range of conditions inhabited by a single species or genera of corals is often broad. The genus *Pocillopora* is illustrative. Stimson (1978) reports that the *Pocillopora* species at Enewetak occur over a broad range of depths but are most abundant on reef flats and in water <5 m deep with currents. He reported *P. verrucosa* to reach 15 m depth on pinnacles and windward and leeward reef slopes and to occur in the "small head zone" (Odum and Odum, 1955) north of Japtan.

Pocillopora verrucosa is also common in spur and groove areas of the windward reefs. In eastern Australia the species is found in areas of regular water movement and good illumination, and its growth variations are less diverse than those of *P. damicornis* (Veron and Pichon, 1976). *Pocillopora damicornis* occupies potentially a greater range of habitats than any other coral at Enewetak. Veron and Pichon (1976) have figured the wide variation in corallum morphology and documented the broad range of conditions this species inhabits in eastern Australia. *Pocillopora eudoxyi* occurs deeper than any other branching coral at Enewetak, to approximately 60 m on the seaward slope.

Members of *Acropora* are similar. Some are limited to very shallow water. Stimson (1978) found *A. aspera* and *A. humilis* only in water less than 2 m deep. *Acropora digitifera* and *A. aspera* are sometimes exposed and killed by extreme low tides. Others, such as *A. syringoides*, are restricted to water deeper than 5 m. *Acropora syringoides* is abundant on the flanks of patch reefs and pinnacles near Enewetak and Medren. Other species have broad depth distributions. *Acropora hyacinthus* and *A. nasuta* occur from 1 to 20 m depth.

Coral growth rates have been examined for a number of species of stony corals at Enewetak. The technique of x-radiography of slabbed coral specimens was first applied to Enewetak coral specimens and used to verify the annual nature of the density banding observed (Knutson et al., 1972). Autoradiographic exposures of coral slabs show distinct bands of activity from atomic test series and, therefore, serve as bench marks in coral growth chronology. Knutson et al. (1972) also presented evidence that the high density bands seen were formed during the rainy season at Enewetak. Buddemeier et al. (1974) examined skeletal growth rates of 15 species of corals, including the same species from various locations at Enewetak. They reported growth rates of generally 4 to 12 mm per year with some exceptions above and below these figures. Not all coral species examined showed variation in growth rates with depth. *Porites lutea* did show a negative correlation between growth rate and increasing depth, with about one-half the rate at 25 to 30 m as was at 4 to 10 m depth. However, colonies of *Goniastrea* sp. collected in deep water grew as fast as those from shallow water.

Although Buddemeier et al. (1974) focused attention on obtaining large symmetric head corals, no specimens examined indicated ages before 1952 and 1953. Whether the nuclear tests of 1952, particularly the "Mike" test, had any effect on this is uncertain.

Stimson and Polacheck (MPRL, 1977) reported that growth rates of *Acropora* and *Pocillopora* at four different depths from 1 to 15 m on lagoon pinnacles and patch reefs were statistically indistinguishable. Three species of common shallow water *Acropora* had annual increments in

diameter of the colony of about 5 to 6 cm, whereas *Pocillopora* in shallow water had an annual growth in diameter of about 4 cm. Smith and Harrison (1977) reported table *Acropora* colonies to increase their diameter 15 cm or more per year once they had reached the stage where they transform from a vasiform to tabulate corallum.

Haggerty (1980) found that with increasing water depth both *Favia pallida* and *F. stelligera* had more widely spaced corallites, a slower linear skeletal growth rate and a decrease in the annual skeletal growth rate per square centimeter. *Favia pallida* had a hemispherical colony form in all environments at 3 to 41 m depth, but deep water populations possessed more septa per corallite than shallow water. *Favia stelligera* changed its colony morphology with depth, from "lobate or hummocky" in shallow water to "columnar with a slight basal skirt" (Haggerty, 1980) in deeper water.

Stimson (MPRL, 1973) looked at the interactions via "extracoelentric digestion" between closely adjacent corals of various species at Enewetak. In the hierarchy of Enewetak corals, based on the species which could be successfully "attacked," *Astreopora myriopthalma* ranked the highest, with *Acropora acuminata* second, and *Porites lutea* third. *Pocillopora* spp. were lowest, being killed on contact with other species.

Stimson (1978) studied the timing of planulation by species of *Pocillopora* and *Acropora* at Enewetak. He found Enewetak colonies to produce planulae primarily during the new and first quarters of the moon. He also suggested that planulation by *Acropora* may be more seasonal than *Pocillopora* because about twice as many colonies planulated during the summer than in the winter. Among pocilloporids, colonies 6 to 8 cm in diameter (15 to 30 cm^3 in volume) were the smallest observed to planulate and estimated to be 1 to 2 years old. *Acropora* colonies as small as 50 cm^3 planulated, but most were greater than 1000 cm^3 in volume. Pocilloporids generally produced more planulae than acroporids at Enewetak. There can also be geographic variation in lunar timing of planulation. The lunar periodicity of planulation in *P. damicornis* is the same in Palau as Enewetak but is reversed from Hawaii (Stimson, 1978).

Stimson (1978) felt that shallow-water corals at Enewetak were in a more "disturbed" environment than in deeper water and that species found predominantly there would have high reproductive rates. He has measured annual mortality rates as high as 20% for shallow-water corals. Most of these species produce planulae rather than smaller eggs and may do so to facilitate rapid settlement in the current-swept reef flat areas.

The large table *Acropora (A. hyacinthus?)* produce shaded area beneath them. Stimson and Polacheck (MPRL, 1977, 1979) found the shaded area to be less than 1 m^2 per colony at 30 to 80 cm from the substrate. The density and number of other coral species beneath table *Acropora*, both dead and alive, were less than in controlled unshaded areas. The genera of corals occurring in the shaded areas were *Stylocoeniella*, *Montipora*, *Seriatopora*, and various massive species. Species of *Acropora* and *Pocillopora* predominated the adjacent unshaded areas.

Kastendick (MPRL, 1975, 1976) examined the habitat differences among eight species of fungiid corals which grow unattached on lagoon coral pinnacles and patch reefs. The young of two species were attached (*Fungia fungites* and *Halomitra pileus*) and found almost exclusively at the upper limit of adult distribution. It is likely that as they age, fungiids move passively down the slope. Kastendick observed invasions of colonies onto the foot area of several pinnacles after removal of these corals the previous year. *Fungia* spp. were found exclusively on coral rubble, whereas *H. pileus* was most abundant on sandy substrate. Translocation of individuals up and down the pinnacle slope indicates that *F. fungites* has the most restricted habitat requirements, with *H. pileus* less so.

Storms during the summer of 1972 (Nolan, 1975; Stimson, MPRL, 1974, 1976) destroyed large areas of coral growth on reefs with a southern exposure, even within the lagoon. Only massive species of *Porites* survived in any quantity on damaged reefs. First recolonizers were *Acropora striata* and *A. syringoides*. Stimson (MPRL, 1975, 1976) also noted that *Sarcophyton* sp., a soft coral, was an important colonist and component of the benthic fauna on storm-damaged reefs. As the hard coral community recovered, he believed that *Sarcophyton* sp. would become progressively rarer. It was observed shading many corals, including *P. damicornis* and *Seriatopora hystrix*.

Highsmith (1981a) suggested that corals with high skeletal density are less able to recolonize dead areas on their skeletons by tissue growth than less dense species. For example, he reports *Porites lutea*, with a relatively low density (1.4 to 1.5 g cm^{-3}), is able to rapidly grow over dead skeletal regions, whereas *Goniastrea retiformis* (1.6 to 2.0 g cm^{-3}) requires considerable skeletal deposition and polyp growth reorientation to overgrow dead areas.

Calcareous material produced by organisms other than stony corals is important in both the reef framework and sedimentary material. Animals, other then Scleractinia, which might make a significant contribution are the Foraminifera, Mollusca, Bryozoa, Sclerosponges, and other Cindaria.

The occurrence of foraminifera tests in sedimentary material in the lagoon and beach sands at Enewetak is well documented (Emery et al., 1954; Odum and Odum, 1955; Deutsch and Lipps, 1976). Forams may consititute a significant percentage of lagoon sediment grains, but they are believed insignificant in reef growth. Mollusc shells similarly constitute a minor component of lagoon sediments but do not contribute to reef growth.

Cuffey (1973) found no bryozoans on the coralline algal ridge of Enewetak and very few in the area (which he terms the "back-ridge trough") immediately shoreward of it. The reef flat, similarly, has almost no bryozoa occurring on it. Areas between islands with abundant coral in shallow water also had relatively few bryozoa. However, in the lagoon margin area, where larger patch reefs begin to

occur, bryozoans increase in abundance, particularly in the patch reefs at depths below 9 m. Cuffey (1973) believed the floor of the deep lagoon, accessible to him only by dredging, lacked any diverse bryozoan fauna and only a few "small detrital fragments" of bryozoa were taken. The pinnacle reefs of the deep lagoon, however, contained an abundant and diverse complement of bryozoans. The steep leeward slope of the atoll apparently had the most diverse community of bryozoa, particularly below 9 m.

Cuffey (1973) found bryozoans more abundant in Bermuda than Enewetak, where they were infrequent in depths less than 9 m. He suggested that the considerably higher diversity of Enewetak corals might adversely influence the relative success of bryozoa when compared to Bermuda. He makes the interesting observation that "the leeward (southwestern) side of Eniwetok Atoll harbors noticeably more bryozoans (both taxa and individuals) than does its windward (northeastern) side. Bryozoan distribution on Eniwetok thus parallels sponge distribution within Pacific atolls, as described by De Laubenfels (1954)." In addition to not being principal frame builders on Enewetak reefs, bryozoans do not contribute any significant amounts of classic detritus to the sediments of the reef (Cuffey, 1973).

Cuffey (1973), in considering the bryozoa of Enewetak, found that most species inhabited the undersides of corals and rocks on reefs. The most abundant bryozoans at Enewetak were encrusting cheilostomes which grow as thin, sheet-like crusts on the undersurfaces of corals or rocks. Most bryozoa inhabited these sheltered microhabitats and "function primarily as 'hidden encrusters,' adding small quantities of calcareous skeletal material to the reef framework." Cavity-filling tendency by bryozoa was noted in Bermuda but not at Enewetak.

Hydrozoans of the genus *Millepora* are extremely important calcifying and reef-building organisms at Enewetak. In many areas, such as the large coral head zone of Odum and Odum (1955), *Millepora* spp. can form heads several meters across which grow to the low tide level where they form flat-topped structures (Fig. 12). In deeper water—including the ocean slopes of all sides, lagoon margin patch reefs, and lagoon pinnacles—*Millepora* spp. form large delicately branched, often fan-like, colonies (Fig 21).

The stylasterine hydrozoans, unlike *Millepora*, are not important carbonate producers at Enewetak. The delicate fan-like species of *Stylaster* are found beneath overhangs and within caves of patch reefs, pinnacles, and on outside reefs. Similar, but more robust, are two species of *Distichopora* which occur in similar areas but are often more exposed. These are extremely common on the leeward reef slope but do not produce reef framework.

Tubipora musica is not common at Enewetak, being found only occasionally on reef fronts or on lagoon pinnacles, and therefore does not produce significant reef structure.

Calcareous green algae, particularly members of *Halimeda*, are extremely important in sedimentation and reef building. The distribution of *Halimeda* in most subtidal environments at Enewetak is well documented (Hillis-Colinvaux, 1977, 1980, 1986; Emery et al., 1954; Colin, 1986). Borings at various atolls (Funafuti, Enewetak, Bikini, reviewed by Hillis-Colinvaux, 1980) have shown *Halimeda* segments to be the major identifiable component of unconsolidated lagoon deposits. Milliman (1974) indicates that among sand-sized components of lagoon sediments in Pacific and Atlantic atolls, *Halimeda* segments are generally the first or second most common material. Hillis-Colinvaux (1980) cites evidence in Couch et al. (1975) that *Halimeda* segments make a significant contribution not only to unconsolidated lagoon sediments but also to material underlying the reef rim. The fate of *Halimeda* plates in sediments varies. Some are shed intact, but a few species (*H. macrophysa* and *H. favulosa* at Enewetak) have delicate segments that are easily broken (Hillis-Colinvaux, 1980).

Carbonate production rates by *Halimeda* at Enewetak are not well known, depending on plant density, generation time, and shedding rates. Hillis-Colinvaux (1980) reports that population densities in *Halimeda* can vary by two orders of magnitude with concurrent effects on carbonate production. Turnover rates are perhaps lower than some published data (Hillis-Colinvaux, 1980) since *Halimeda* is predominantly a long-lived alga. One experiment at Enewetak indicated that 70% of the original thalli were still present after 4 months (Hillis-Colinvaux, 1980).

Dense populations of *Halimeda* at Enewetak and elsewhere have about 100 plants m^{-2} of the *H. incrassata-cylindrica* type thallus. The rock-growing *H. opuntia* type can have higher densities of plant material, although absolute numbers of plants may be less. Hillis-Colinvaux (1980) estimates that the *H. incrassata-cylindrica* types would produce only about 10% of the total carbonate accumulation in the lagoon (Smith and Kinsey, 1976) if they covered the major portion of the lagoon bottom. She was not aware at that time of the presence of the "*Halimeda* meadows" and the estimated percent coverage of the deep lagoon bottom predominantly by *Halimeda*. The contribution of *Halimeda* segments from lagoon pinnacles may be smaller than Hillis-Colinvaux (1980) calculated when a comparison was made to *Halimeda* from flat lagoon bottoms.

Bioerosion of Reefs

The agents of bioerosion at Enewetak act in a variety of ways. Some, such as the boring sponges of the genus *Cliona*, excavate chambers on the carbonate skeletons of living corals and virtually any other carbonate substrate. The shells of molluscs, coral rubble, and other small carbonate fragments can be attacked. Other organisms, in the course of feeding activities, rasp away the surface layers of carbonate while grazing the thin film of algae which covers such surfaces. The parrot fishes, surgeonfishes, various echinoderms, and other such herbivores generally pass the carbonate material through their gut, subjecting it not only to mechanical effects but also to chemical effects. Other

organisms may prey directly on calcifying organisms and in the process often damage the skeleton.

A few species of fishes vigorously attack coral skeletons, biting off and ingesting the tips of branched species. Randall (1974) observed the pufferfish, *Arothoron nigropunctatus*, feeding heavily (85 to 100% of gut contents) on corals, particularly *Acropora* and *Montipora*. Hiatt and Strasburg (1960) found corals in the guts of nine plectognath fishes (two triggerfishes, three filefishes, three puffers, and one sharpnose puffer). Most, but not all individuals of any species, had ingested branched coral tips in various amounts. Although none of these fishes are obligate coral predators, many contain coral tips in such quantity that these must constitute a regular part of their diet at Enewetak (Randall, 1974).

Large portions of coral skeleton will, on occasion, have the ends of the branches removed, often with piles of coral fragments left in the depression. This is seen in *Porites rus* at Enewetak (Fig. 21) and in other species. It is assumed this phenomenon results from the activities of fishes which feed on coral branches, but the feeding by some of these fishes is seldom observed.

Other coral-feeding fishes tend to eat only the polyps, leaving the skeleton essentially intact. In such cases, the polyp normally regenerates. A number of butterflyfishes (Chaetodontidae) and damselfishes of the genus *Plectroglyphidodon* feed on corals in this matter (Motta, 1980; Randall, 1974; Reese, 1973, 1975, 1977) and are discussed elsewhere. Randall (1974) notes also that the blenny *Ecsenius bicolor* at Enewetak has been observed feeding on *Acropora*.

Some herbivorous fishes occasionally scrape at the surface of living corals doing more damage than the chaetodontids. Scarids produced a characteristic scrape mark on corals with an elongate furrow, often with a slight ridge along its midline where the two sides of the beak fuse. Hiatt and Strasburg (1960) found some species of scarids at Enewetak had fed on corals. Randall (1974) has reviewed the question of parrot fish grazing on live corals and discusses an apparent disparity between published data on coral feeding by scarids at Heron Island, Great Barrier Reef, and Hiatt and Strasburg's (1960) information. He found no obvious reason for the differences observed but suggested that local coral cover may influence how much coral is ingested by parrot fishes. Although some scarids do graze live corals, the impact of this behavior is probably minor compared to the effect on sediment production and deposition.

Randall (1974), Ogden (1977), and others have documented the role of scarids in sediment production. The rasping of rock or coral for its algal film is the first step. This material is then ground to a fine consistency by the pharyngeal mill of the parrot fish, passed through the gut, and eventually expelled. The rain of sedimentary material shed when parrot fishes defecate is impressive, and the amount of sediment produced from hard substrates by this mechanism is enormous.

Also important in sediment production are fishes which reduce the hard parts of invertebrates (mollusc shells, echinoid tests and spines, crustaceans, etc.) to bits. Randall (1974) reports that plectognaths with their fused or buttressed teeth, lethrinids with molariform teeth, labrids with pharyngeal teeth, and dasyatid and myliobatid rays with plate-like jaws are well adapted for this purpose.

Massive corals at Enewetak are attacked by a number of biological agents. Although seldom visible, these agents weaken the skeleton to the point that physical factors can break the colony loose or cause it to crumble. Highsmith (1981a) reports that clinoid sponges accounted for 70 to 80% of skeletal damage in various massive corals from Enewetak. They did not burrow deeply into the skeleton, only a few millimeters, but extended interconnected chambers laterally beneath dead surfaces of the coral colony. Highsmith (1981a) reported that 65 to 95% of the boring was within the "dead area" of skeletons. In a massive coral this "dead area" includes the area around the basal attachment and dead spots on the colony surface. Similarly, these dead areas are heavily eroded by grazing organisms. When exposed to light or scraped (as when overlying skeletal material is removed), clinoid sponges engage in rapid burrowing (Ruetzler, 1975). Heavy grazing pressure, combined with this response, may produce rapid erosion rates at basal attachments.

Highsmith (1981a) points out that skeletal weakening at the base, combined with storm-induced water motion, may not be sufficient to dislodge most massive colonies. However, coral rubble on the bottom can be put into motion by storm waves and, to a point, may be the most significant force in breaking heads loose. Eventually though, "as massive corals grow, they become more susceptible to breakage by storm currents and less susceptible to breakage by suspended rubble or to bioerosion detachment."

The alpheid shrimps occurring in deep grooves on *Goniastrea retiformis* apparently form the grooves, not by boring or erosion, but by preventing growth of coral in that area while the remainder of the colony continues to increase in size (Fig. 22). These grooves, though, provide dead areas which penetrate deeply into the *G. retiformis* head and are penetrated by boring organisms (Highsmith, 1981a).

Highsmith (1981b) suggested that bioerosional damage to corals is positively correlated with increasing skeletal density. Five species of Enewetak corals (*Oulophyllia crispa, Favia pallida, Goniastrea retiformis, Pavona clavus,* and *Porites lutea*) had a positive correlation between bioerosion and density. This correlation did not correspond to differences in growth rates. The slowest growing species, *F. pallida*, was the least bored.

Among molluscs, the boring bivalve *Lithophaga curta* preferentially colonized the coral *Montipora berryi* (Highsmith, 1980). Boring bivalves in general have thin, weak shells and, if exposed, are easily eaten by fish predators. Highsmith (1981a), for example, reported that the

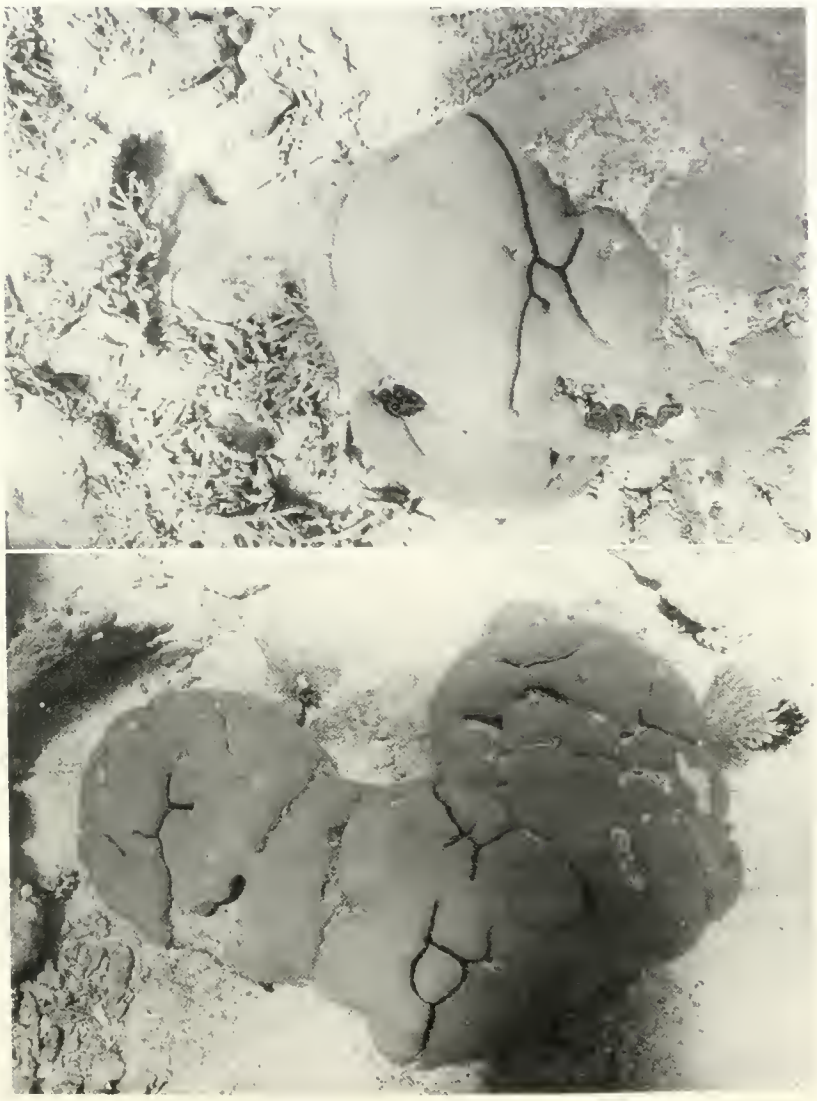

Fig. 22 Heads of *Goniastrea retiformis* with deep grooves formed through the activities of alpheid shrimps.

wrasse *Thalassoma lutescens* readily took bivalves exposed during collecting. Bivalves were not common borers of Enewetak massive corals. Highsmith (1981a) found only four bivalves in more than 100 coral heads and contrasts with other areas where they produce significant boring.

Polychaetes are also significant borers of corals (Highsmith, 1981a) but are often believed to occupy empty sponge chambers. He found 280 polychaetes in a single *Porites lutea* head; the diversity of polychaetes exceeded any other infaunal organisms. Although they are common, they are probably not as important borers as are sponges. Sipunculans were important borers of coral rubble, rather than live coral (Highsmith, 1981a).

Highsmith (1981b) discussed the role of endolithic algae, *Ostreobium* spp., in several species of Enewetak corals. They occur as one or more dark green bands in the upper few centimeters of the coral skeleton. He found *Ostreobium* in every coral sampled from the surface to 30 m depth. No significant effect by the filamentous algae on the integrity of coral skeletons was detected. In some species of corals there was an inverse correlation, with considerable variation, between water depth of a coral and the depth of its outermost algal band. Algal bands are believed to occur where and when conditions are suitable for vigorous growth.

DiSalvo (1969) isolated bacteria from within the skeleton of the coral *Porites lobata*. Bacteria were cultured from light brown discolored regions revealed when the corals were split open. Attempts to culture bacteria from adjacent, nondiscolored skeleton were not successful. Some of

the isolated bacteria were able to digest chitin in vitro, and DiSalvo suggested these might weaken the skeleton by breaking down the organic matrix. DiSalvo (1969) also found that sediments in proximity to the bases of corals had 10^7 to 10^8 bacteria g dry wt^{-1} of which 10 to 20% were chitin-digesting varieties. Thus there is a ready source of suitable bacteria close to the coral's skeleton.

Invertebrate Coral Predators

Some invertebrates are also coral predators at Enewetak. The crown-of-thorns starfish, *Acanthaster planci*, is found in many areas. Most lagoon pinnacles have one or more *A. planci*, and evidence of their feeding activities on corals is apparent. The status of *A. planci* populations at Enewetak, population changes, and impact on the reefs in recent times are not well known. Population levels are certainly below "plague" levels. Allen (1972b) noted that "during the summer of 1970 the author observed an increasing number of *Acanthaster* at Eniwetok. Prior to this date relatively few were observed." Starck (MPRL, 1971, 1972) found "no unusual populations of *Acanthaster*." About a 1-hour (one dive) search during the day would result in one to two individuals, whereas a nighttime search of about only one-quarter the area revealed 10 to 12 specimens. Starck found a wrasse, *Cheilinus undulatus*, of about 50 kg weight (of four examined) with a large, nearly intact *A. planci* in its gut contents. Starck, in Anderson (1979), reported a sizeable population, perhaps as many as 50 to 100 *A. planci* on Pole Pinnacle, but stated that there was no extensive damage to the coral there.

The juveniles of *A. planci* apparently occur beneath rubble on reefs. Lisa Boucher and Scott Johnson (personal communication) report finding numerous examples from a few centimeters to less than 1 cm disk diameter on pinnacles near Enewetak Island. Although they never found these *A. planci* to be very common, a distinct increase in the numbers of juveniles encountered was noted in April 1982.

Storm Destruction of Reefs

The effect of subtyphoon storms (tropical storms, tropical depressions) on subtidal environments can be devastating. Many such storms occur compared to full strength typhoons and are often not noted in historical records. Damage from wind and rain to terrestrial areas may be minor, but the swell produced by such storms can wreak havoc in shallow-water communities. The production of boulder ramparts by storms is well known, and such structures occur on the southwest islands of Enewetak. Since the ocean shores of these islands are normally in the lee and the reef slope is steep and close to shore, the infrequent reversal of wind and waves can cause catastrophic destruction of corals in shallow water, moving vast quantities of material onto the shore or into deeper water.

The movement and effect of ocean swells in the lagoon are important. The wide pass at Enewetak is sufficiently deep to allow ocean swell from the southeast to southwest to enter the lagoon. Ocean swell is also refracted at the pass so that wave trains moving from the west and southwest can come through the pass and proceed north to northeast to reach lagoon shores. These long period swells have no direct effect on the deep lagoon communities. However, when they reach the lagoon shore of windward islands or shallow pinnacle or patch reefs, they can turn these shallow-water communities into churning maelstroms of breaking waves. One such period of swells from the southwest to west for 3 days in July 1982 turned the lagoon shore of Enewetak Island and other southern islands into a mass of dark brown water (with essentially zero visibility) above 6 m depth with breakers to 2 m high where depths were less than about 4 m. Significant swells and breakers persisted for nearly 1 week. Many fishes, molluscs, and other invertebrates were killed and cast up on the beaches. In places sediment and rubble were eroded away as much as 1 m or more. Many of the delicate corals on shallow reefs (*Pocillopora edouyxi, Millepora* spp.) were broken to stubs.

Carbonate material from shallow water, particularly large pieces such as coral boulders, can be deposited on the islands by storm waves, transported into the lagoon or transported downslope on the seaward reefs. Various islands of Enewetak are densely covered with recently deposited coral boulders, and boulder ramparts are evident on the seaward beaches of some islands. Less visible, but perhaps more significant, is downslope transport of rubble on seaward reefs. Talus was evident at many locations examined by the submersible *Makali'i*, and shallow-water coral rubble was extremely evident in the material photographed. At 300 to 360 m, the maximum depths visited, the slope of the bottom was generally too steep for extremely large talus accumulations. Larger accumulations of talus should lie below those depths where the bottom slope is less steep.

Storm swell within the lagoon may be a major factor controlling the morphology of lagoon margin patch reefs and shallow pinnacle reefs. Choptop Reef had moderate damage from swells entering the lagoon in July 1982. Some large coral heads, their bases weakened, were tumbled over. Pieces of *Porites cylindrica* colonies as much as a meter across were torn loose from larger colonies and rolled a few meters over the bottom. Although individual branches were often broken, such pieces formed satellite patches of *P. cylindrica* which survived and grew. In another instance, a tunnel torn through a huge mass of *P. cylindrica* at Choptop Reef during a tropical storm in March 1981 was collapsed by the July 1982 storm. In both instances the total structure was fractured. Swell within Enewetak Lagoon seems capable of breaking apart patch reef features which reach too near the surface. Where the internal structure of lagoon margin patch reefs is visible, they seem little more than accumulations of poorly cemented coral rubble. One well-known lagoon pinnacle, "Tunnel Pinnacle" (Fig. 6), has had the "tunnel" collapsed, almost certainly by storm swell, during the past few years. Reese (1981) provides a description of the

effects of storms on the corals and butterflyfishes (chaetolontidae) of "Tunnel Pinnacle" and other pinnacles at Enewetak.

The lack of significant cementation on upper surfaces of patch reefs and pinnacles by coralline algae may reduce greatly the amount of wave energy required to crumble the structure. Protection of the lagoon from storm swells by a complete or nearly complete atoll rim with no deep passages may also be important. At Ujilang Atoll, which has no major passes allowing ocean swell to enter the southern lagoon, lagoon margin patch reefs examined were near planar on top at about the level of spring low tides with near vertical edges dropping to a few meters in depth. The patch reefs were well cemented by coralline algae on their upper surfaces. Ujilang is exposed to essentially the same oceanic conditions (wind, waves, and storms) as Enewetak, yet patch reefs of such morphology are not found at Enewetak.

Herbivory in Subtidal Communities

Much work on herbivory and its impact on the ecosystems at Enewetak has been undertaken on intertidal areas because of the large, accessible area of such environments at the atoll and the abundance of herbivores there. Herbivory is a major factor influencing subtidal communities in the lagoon and on the seaward margin. Evidence of intense grazing pressure can be found in many subtidal areas, both on hard and soft substrata.

Unlike the intertidal areas, subtidal areas are accessible to herbivores at all times. On exposed rock substrates, both seaward and lagoonward of the reef flat at Enewetak, tooth marks from the action of grazing fishes are nearly ubiquitous in areas to at least 15 to 20 m depth. Many show considerable erosion from grazing (Fig. 23) with angular facets on the rock, and deep tooth marks, particularly from large parrot fishes, are often densely grouped.

The principal grazers of hard substrates at Enewetak are fishes, particularly parrot fishes (Scaridae) and surgeonfishes (Acanthuridae). In general, algae on subtidal rock surfaces are close-cropped except in the case where the species may be heavily calcified (*Halimeda* spp.) or potentially toxic or distasteful (*Lyngbia* sp.). In this respect subtidal rock surfaces are not qualitatively different from the intertidal reef flat. Macroalgae and algal films are found at all depths in the lagoon.

Surgeonfishes show a well-defined zonation among this largely herbivorous family. *Acanthurus triostequs*, *A. achilles*, *A. guttatus*, and *A. lineatus* are principally found on windward and leeward reef flats, back reef areas, and the spur and groove zone—all shallow-water environments. In somewhat deeper water on the seaward reefs, lagoon patch reefs, and pinnacles are found species of *Ctenochaetus*, *Zebrasoma*, *Acanthurus nigrofuscus*, and *A. olivaceus*. Two species of *Acanthurus* at Enewetak, *A. thompsoni* and *A. bleekeri*, feed on zooplankton as do most species of *Naso*. The species of surgeonfishes with a well-developed gizzard-like stomach commonly feed on sediment bottoms and ingest, along with the algae, considerable sand (Randall, 1956; Hiatt and Strasburg, 1960) (Fig. 23).

Herbivory occurs on sediment bottoms where macroalgae and microalgae occur. Macroalgae can occur as dense stands, as exemplified by the species of *Halimeda* and *Caulerpa*, and many are probably unpalatable to herbivores. Microalgae can occur as nearly invisible films on sediment grains on the surface of the sediment bottom, but easily apparent films (algal mats) covering many square meters are often found from a few meters depth to the deepest portion of the lagoon. Epiphytic algae also grow upon larger algae and are often more desirable to herbivores than the plants on which they grow.

Invertebrate grazers of rock surfaces are not as important at Enewetak as in the western Atlantic. In many Caribbean locations sea urchins, particularly *Diadema antillarum*, are extremely abundant and as herbivores have an impact equaling, or exceeding, that of fishes (Ogden, 1976; Ogden and Lobel, 1978). Sea urchins, particularly diademnids, are not nearly as abundant, except in localized areas, on reefs at Enewetak.

Fishes are important herbivores of sediment bottoms at Enewetak. The principal herbivore families of hard substrata, parrot fishes and surgeonfishes, range onto sediment bottoms also (Fig. 23). Different species from those that remain on the reef are often involved. As distance increases from the shelter of the reef, the grazing pressure of reef-based herbivores decreases. They are exposed to increasing risk of predation with increasing distance from shelter. Therefore, soft bottoms near reef shelter are more heavily grazed, often to the extent that no visible benthic plant growth except the less desirable species mentioned previously occur near the reef. This results in a phenomenon most easily visible from the air in which reefs are surrounded by a light colored band, compared to sediment substrata farther away, representing the denuded substatum close to the reef. This area has been termed a "halo" (Randall, 1965) or the "Randall zone" (Ogden, 1976) and is a feature found near both Indo-West Pacific and Atlantic reefs.

Other herbivores, particularly invertebrates, exist far from the reef, either remaining on or above the sediment surface or burying and burrowing in the bottom. Dense stands of macroalgae provide excellent shelter for small herbivores, both fishes and invertebrates which can hide among the thalli. Although these macroalgae are not primary foods for these herbivores, the environment created provides abundant spaces for epiphytic algae (and epizoic organisms also) which are suitable for the small herbivores.

In areas without dense algal cover, burrowing organisms can function as herbivores without the need of shelter. Irregular sea urchins (Spatangoidea) occur abundantly in Enewetak Lagoon sediment bottoms and apparently process sediment grains for the algal matter on their surfaces. These and other "sediment processors" must pass relatively large amounts of sediment to obtain sufficient organic matter.

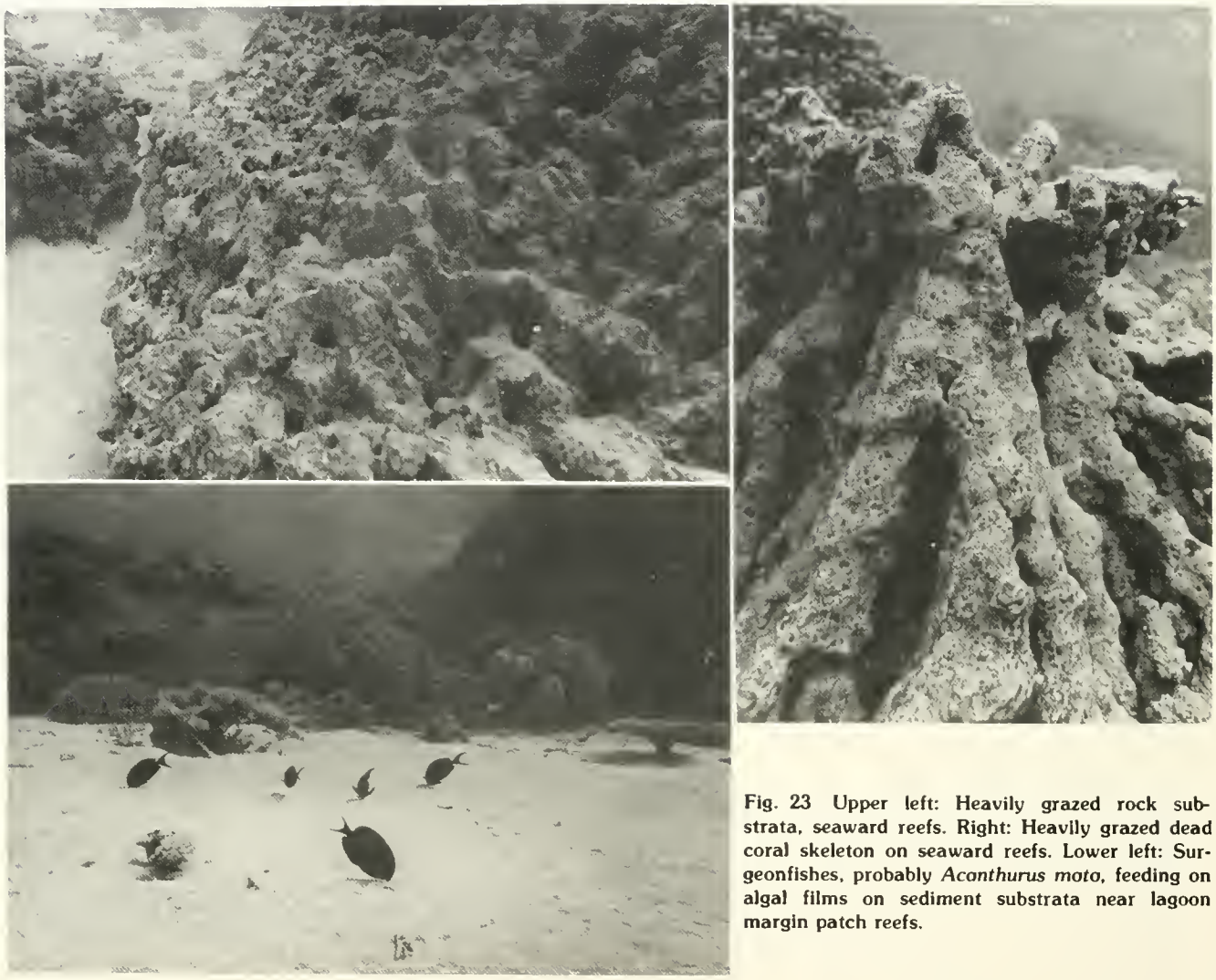

Fig. 23 Upper left: Heavily grazed rock substrata, seaward reefs. Right: Heavily grazed dead coral skeleton on seaward reefs. Lower left: Surgeonfishes, probably *Acanthurus mata*, feeding on algal films on sediment substrata near lagoon margin patch reefs.

Other herbivores are found on the sediment surface. The gastropod, *Strombus luhuanus*, can occasionally occur in localized high densities over open sediment in water 2 to 10 m deep. Densities more than 10 individuals per m^2 with distinct (advancing?) edges to the population were often seen with adjacent areas lacking *S. luhuanus*. High densities of *S. luhuanus* have been found at stations where only a few weeks previously the species was absent.

Numerous species of sea cucumbers (Holothuroidea) are found on sediment—sometimes near reefs, but not always. They process sediment through their gut and are relatively immune to predation, probably because of their toxin (holothurin). Lamberson (1978) found the relatively large species (up to ¾ m in length) *Thelenota anax* in relative abundance at Enewetak at 5 to 30 m depth. This species was found on lagoon pinnacles and patch reefs, on sandy bottoms near reefs, and on the vertical slope off the leeward side near Biken.

Holothurians are important sand processors of reef areas. Bakus (1963) reported that *Holothuria dificilus* ingested sediment particles up to 2 mm in size, but about 80% were less than 250 microns in diameter. *Holothuria atra* fed on even larger rubble, up to 20 mm in size. Bakus (1973) indicates that beyond selection of suitable size, there is little specificity among tropical holothurians for sediments ingested. Hammond (1981) found that among West Indian holothurians and echinoids (irregular) that significant carbonate dissolution and sediment grain-size modification did not occur during passage of sediment through the guts of five species of tropical deposit-feeding echinoderms. A similar situation probably exists for Enewetak species.

Irregular urchins are important herbivores of open sandy areas. Extremely high densities (more than 50 m^{-2}) of moderately large (more than 30 to 35 mm test length) species have been observed over large areas. This implies

that a significant amount of algal production must be available for them to survive for any period. Population size of irregular urchins seems influenced more by recruitment success than by food availability (V. S. Frey, unpublished data).

There are many other organisms living in the sediment which ultimately make their living from the algal production occurring on sediment surfaces or passing over the sediment. The callianassid crustaceans, mentioned previously for their bioturbational activities, almost certainly process prodigeous quantities of sediment to winnow the organics present on the surface of the sediment grains. They may additionally exploit the algal fragments which enter their burrow systems.

On hard substratum, some herbivores at Enewetak live within a limited area which they maintain as a territory. Some damselfishes, particularly *Stegastes nigricans*, establish and maintain an "algal lawn" of filamentous algae. The algal lawn is often found on basal dead parts of the fine branches of *Acropora* spp. corals and is strongly defended against intruding herbivores. This action by *S. nigricans* is identical to the western Atlantic *Stegastes planifrons*, the first species for which algal lawn maintenance was described (Kaufmann, 1977). It is likely that *S. nigricans* can kill coral polyps in expanding its algal plot, and large numbers can significantly damage *Acropora* spp. corals. The darkened areas of damselfish algal plots are common features of *Acropora* spp. thickets at Enewetak (Fig. 24). The long-range effect of these areas of dead coral has not been examined, though areas a few meters square of dead *Acropora* are often found in the midst of dense thickets (Fig. 24). These may potentially represent old algal plots eroded away by other herbivores.

The general lack of herbivores as significant as fishes at Enewetak presents an interesting contrast to reefs in some other areas of the world. In the tropical western Atlantic, sea urchins, particularly *Diadema antillarum*, play a role as herbivores equal to or superior to that of fishes

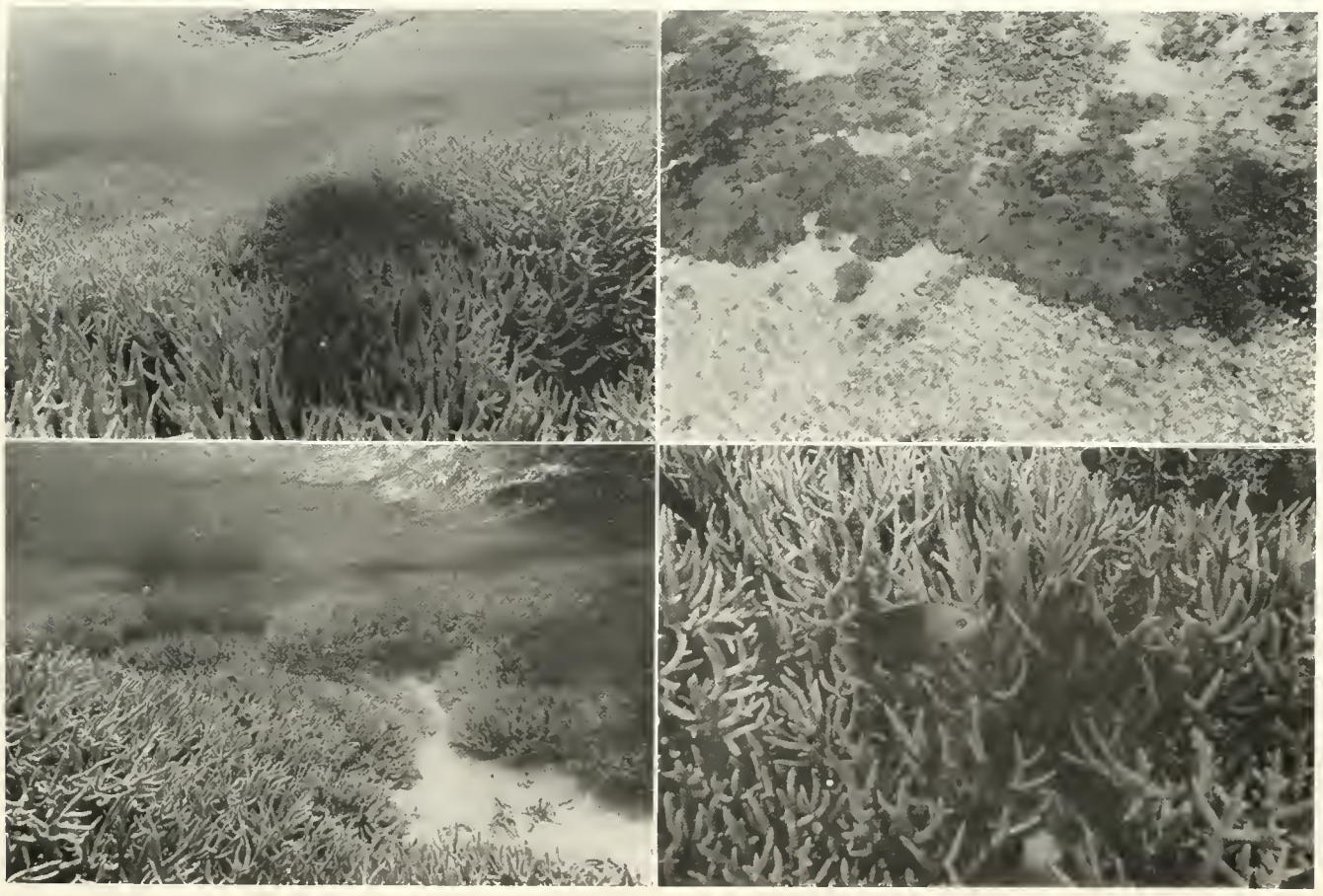

Fig. 24 Algal "lawns" on *Acropora* sp. corals produced by the herbivorous damselfish *Stegastes nigricans* in the Enewetak Island quarry. Upper left: Large dead area in the *Acropora* sp. coral possibly produced by the presence of an algal lawn. Upper right: Aerial view of Enewetak quarry *Acropora* sp. with many algal lawns (dark spots) established on the coral. Lower left: *Acropora* sp. coral in the quarry with algal lawns. Lower right: *Stegastes nigricans* with its algal lawn (dark area to right of fish).

(Ogden, 1976). Sea urchins are abundant and conspicuous elements of the reef fauna. At Enewetak and much of the Indo-West Pacific, sea urchins are considerably less abundant. Diademnids are particularly less conspicuous, being small and deeply hidden in the reef. One possible explanation for this difference is a higher population of fishes which prey on sea urchins in the Indo-West Pacific (Fricke, 1971). In general, western Pacific fish faunas are considerably more diverse and "highly evolved" than the Atlantic, and more species may be adapted for exploiting sea urchins (among other things) as food.

Gilmartin (1960) indicated that herbivores have a much smaller influence on benthic algal communities at 19 to 63 m at Enewetak than they do on shallower communities. Bakus (1967) felt that grazers influence the benthic biota most in water <10 m deep.

With heavy grazing pressure from herbivores, the presence of dense abundant algae implies some reason for its avoidance by herbivores. For example, the filamentous strands of the blue-green algae, *Lyngbia* sp., occur extremely abundantly on projections, particularly corals; on many reefs at depths below 6 to 9 m on windward lagoon reefs; and as shallow as 1 m in protected areas. The alga covers large areas of the substratum, streaming from corals and resembling long reddish hair. Often it virtually covers the coral with a tangle of filaments that is extremely difficult to remove. *Lyngbia* sp. often seems to have detrimental effects on the live coral with the coral tissue beneath the algae appearing unhealthy. Often coral areas beneath the alga are dead, but whether the alga is the causative agent or simply grows on available substratum is not known. At some lagoon pinnacle reefs, such as Medren Pinnacle, *Lyngbia* sp. appears to have a significant impact on the total reef and may be significant in coral mortality there. *Lyngbia* sp. is also abundant on some lagoon margin patch reefs below 6 m depth but is absent on the shallower portions of the same reefs.

The small sea hare, *Stylocheilus longicauda*, occurs abundantly on the *Lyngbia* sp. Sarver (MPRL, 1976) reported it feeds almost exclusively on *Lyngbia* sp. and spends its life, exclusive of larval stages, on the alga. The sea hare accumulates an antitumor agent, debromoaplysiatoxin, from *Lyngbia* sp. and *Oscillatoria* sp. at Enewetak. This poisonous lipid was first isolated from the digestive tract of *S. longicauda* but has its origin from the blue-green algae (Moore, MPRL, 1976). Sarver found that adult *S. longicauda* (about 3 to 7 g) reproduce rapidly, at about 30 days age, and consume about 75 to 100 g of the alga during their lifetime.

Bioturbation in the Deep Lagoon

A high level of bioturbation in sediment bottoms throughout the deep lagoon has been verified by recent work (Suchanek and Colin, 1986; Suchanek et al., 1986). Gilmartin (1960) first noted, based on in-situ observations, significant bioturbation of deep lagoon bottoms, but several other authors have commented on it. Emery et al. (1954) noted, in shallow lagoon photographs, disturbance of the bottom and burrowing. Hillis-Colinvaux (1980) noted a "relative prominence of animal mounds and castings on the lagoon floor near the base of pinnacles in 40 m."

Bioturbation of the deep lagoon is evidenced by the ubiquitous presence of "lebensspuren," a term designating any sedimentary structure produced by a living organism (Hantzschel, 1962). A wide variety of lebensspuren occurs on sediment bottoms at Enewetak, but the conical mounds of ghost shrimps (Callianassids) that are as much as 1 m in diameter and 30 to 40 cm high are the most apparent type. The conical mounds represent the excurrent openings of complex burrow systems which penetrate deep into lagoon sediments and underlie nearly all the sediment bottoms.

Photographs from the Enewetak Lagoon benthic survey, observations from the submersible *Makali'i*, and scuba diving on the lagoon margin have confirmed the near pan-lagoon (below 10 m depth) distribution of callianassid mounds. The basic morphology of the burrow system, pumping rates, and sediment processing have been examined and will be discussed subsequently. Since the lagoon sediments are the major repository of remaining radionuclides at Enewetak, an understanding of the mixing and resuspension abilities of lebensspuren-producing organisms, particularly callianassids, is of basic relevance in any consideration of the future fate of long-lived radionuclides in the marine environment.

Callianassid mounds are often referred to as "volcanoes" because of their conical shape with steeply sloping sides, a small apical depression (crater), and the resulting eruption when water and sediment are pumped out of the apical depression at irregular intervals. These volcanoes can be so dense that essentially no level substratum can be found in a large area, the bottom being comprised solely of volcanoes and incurrent depressions of the callianassid burrow systems. It is estimated, based on the photographic survey, submersible work, and diving observations that about one volcano per square meter occurs overall in the lagoon below 10 m depth. Since approximately 85% of the lagoon bottom is soft substratum and covers about 8×10^8 m^2, on the order of 10^9 callianassid volcanoes occur in the Enewetak Lagoon. Densities may vary from place to place by a factor of 10, and several species of callianassids are certainly involved.

A typical callianassid burrow system at Enewetak consists of three major elements: (1) conical depressions on the surface where sediment enters the system, (2) a complex network of horizontal and vertical burrows, and (3) conical mounds (volcanoes) where sediment and water are discharged. The incurrent openings to the system (Suchanek and Colin, 1986), in which sediment and water are drawn into the system, appear as a conical depression many centimeters in diameter. The excurrent side of the system is represented by the volcanoes, each of which is fed by a vertical tube at its center through which sand and water are pumped by the action of ghost shrimp in the

tunnels below. Burrow systems linking the down holes with the volcanoes are complex, often consisting of a series of interconnected horizontal tunnels (as much as 4 to 5 cm in diameter), and sloping to vertical tunnels connecting different levels. As much as 1300 g of sediments were ejected per day from each volcano. Callianassids alter grain size distribution of processed sediment to produce a very consistent sediment size fraction which is depleted (compared to some other Enewetak sediments) in both coarse (>2 mm) and fine (<90 microns) sediments (Suchanek and Colin, 1985). As much as 3 liters of water evolves daily from volcanoes during sediment-pumping activities (Colin et al., 1986). Volcano water contained suspended particulates >0.45 microns in diameter at levels at least five times that of water immediately overlying the sediment, which itself has elevated particulates compared to "average" lagoon water (Colin et al., 1986).

"Tagged" (painted with fluorescent paint) sediment experiments have demonstrated that most large particles, more than 1.5 to 2 mm in diameter, entering the ghost shrimp burrow system are not returned to the surface (Suchanek et al., 1986). Probably such particles are too large to be temporarily suspended by pumping, and it is believed that callianassids "store" large particulates in unused portions of the burrow system.

A constant "disturbance" effect occurs in bioturbation at Enewetak. The constant grazing by herbivores, the digging into the sediment by carnivores looking for prey, and the ingesting and then expelling of sediment by the surface-dwelling species cause the upper few centimeters of sediment to be constantly disturbed (Suchanek and Colin, 1986). The sediment surface, through this action, is a continuous mosaic of small pits and mounds, disturbed places and tracks, all from this surface reworking. In the lagoon at depths shallower than about 5 to 6 m, this evidence is quickly obliterated by wave ripples, but below that depth the disturbances remain apparent for some time.

FISH COMMUNITIES

The fish fauna of Enewetak is quite diverse, numbering more than 800 species. There are, certainly, a number of species yet to be recorded from the atoll. Fish species are not evenly distributed around the atoll; many occur commonly in only one type of habitat. These preferences result in general fish communities which are identifiable assemblages of species. Hiatt and Strasburg (1960) made the first (and still best) attempt to characterize fish communities of various areas of Enewetak and to examine their trophic relationships. Subsequent researchers have examined feeding by various portions of the Enewetak fish fauna (Hobson and Chess, 1978; Randall, 1980; Bakus, 1967; Gerber and Marshall, 1974; Smith and Paulson, 1974; Reese, 1975, 1977; and others), but a definitive study of the overall trophic dynamics of fishes has never been undertaken.

Randall has reviewed records of fishes since Schultz and collaborators (1953 to 1966), and a checklist is included in Chapter 27 of Volume II, this publication. Although this may be approaching a definitive list of fishes for the Marshall Islands for shallow-water species, it was apparent from the observations and photographs from the submersible *Makali'i* that a significant number remain to be recorded (many undoubtedly undescribed) from depths greater than those usually penetrated by scuba divers.

The species of fishes inhabiting a given location at Enewetak are strongly influenced by environmental factors. Primary among these are substratum types (hard or soft, variations of these), depth, current, wave action, and others. The food of Enewetak fishes is based on two different sources: primary production from atoll bottoms and waters and oceanic zooplankton and phytoplankton. The relative importance of these two pathways has never been rigorously compared, but the high productivity of reef flat and lagoon versus the low density of phytoplankton and zooplankton in oceanic water upcurrent of Enewetak imply that the former is of considerable significance. Seeing the immense numbers of large, herbivorous fishes on spur and groove, reef flat, and shallow patch reefs impresses one with the amount of fish life supported by algae growing on the substratum.

Predators of mid- and upper-water lagoon areas are varied. Hiatt and Strasburg (1960) differentiate mid- and surface-water communities but point out that some large carnivores enter both areas. They felt that surface water communities contained various sizes of zooplankton, small plankton-feeding fishes (round herring and silversides), larger macroplankton-feeding fishes (such as halfbeaks), and piscivores (needlefish, tunas, barracuda, jacks). Randall (1980) and Hiatt and Strasburg (1960) have discussed the food habits and general habits of many of these.

The Carangidae are important predators at Enewetak. The members of the genus *Caranx* are largely fish eaters, occasionally taking cephalopods or crustaceans. *Caranx ignobilis*, the largest species of the genus, reaches 80 kg, and as Randall (1980) notes "may be encountered anywhere in the atoll environment including water surprisingly shallow for such a large fish." *Caranx melampygus* is very common on Enewetak reefs and feeds largely on reef fishes, including some such as *Caracanthus* sp., that live deep within the branches of living corals. The rainbow runner, *Elagatis bipinnulatus*, is a mid-water feeding carangid which occurs in schools above reefs.

Among scombrid fishes, the dogtooth tuna, *Gymnosarda unicolor*, is the only tuna commonly seen around lagoon pinnacles. It also occurs on outer reefs and is a predator on free-swimming fishes, including *Naso* spp., *Caesio*, *Pterocaesio*, and *Decapterus* (Randall, 1980). Hiatt and Strasburg (1960) reported it and the common little tunny, *Euthynnus affinis*, as slashing through the dense schools of round herring.

Some species of moderately large fishes are detritivores. Mullets are common on shallow reefs, both lagoonward and seaward of the reef flat. *Crenimugil crenilabis* has

been seen to expel sand through the gills after feeding, a process in common with many smaller fishes, and appears to feed on fine algae detritus (Randall, 1980).

The largest planktivorous bony fish at Enewetak is probably the milkfish, *Chanos chanos*, which occurs occasionally on outer reefs and in the lagoon. The largest planktivore, at least within the lagoon, is the manta ray, *Manta alfredi*. They frequent lagoon margin areas, often in water 3 to 6 m deep, and the wide channel area. On one occasion, a group of more than 100 *M. alfredi* with a 2 m or more span were seen from the air in the deep ocean just beyond the wide channel.

Randall (1980) has summarized the food habits of larger groupers (Serranidae), snappers (Lutjanidae), and emperors (Lethrinidae). All are benthic predators, although some groupers and snappers will rise to a lure in mid-waters.

Large oceanic predatory fishes occur commonly around Enewetak. Tunas, wahoo *(Acanthocybium solanderi)*, dolphin *(Coryphaena hippurus)*, and billfishes are known to frequent waters within a few kilometers of shore (Schultz et al., 1952). Hiatt and Strasburg (1960) note that the presence of larval fishes and crustaceans produced by reef- and shore-dwelling adults, "supplementing the usual high seas forage species, probably is significant in attracting tunas (and other large pelagic fishes) to mid-ocean islands."

There are numerous fishes that are highly specialized in their food habits. For example, in the Chaetodontidae, Reese (1975, 1977, 1981) found that at Enewetak, 10 of 17 species are coral-feeders, whereas two are planktivores and five are "omnivores." Among coral feeders, four were believed to be obligate coral predators, with fine comb-like teeth for biting off coral polyps. One species, *Chaetodon ornatissimus*, appears to eat coral mucus with its fleshy lips rather than biting off the polyps like other species. Other coral-feeding species at Enewetak ingested other animal matter as food. The other extreme is *C. unimaculatus* which even ingests fragments of septa as it feeds on polyps.

Other coral-polyp feeders include *Oxymonocanthus longirostris*, *Labrichthys unilineata*, and *Labropsis* spp. Some damselfishes, such as *Plectrogylphidodon johnstonianus* and *P. dickii*, have been observed to feed on coral polyps (Randall, 1974).

Few Enewetak fishes feed on sponges. Hiatt and Strasburg (1960) recorded only *Arothron mappa*, a puffer, as having eaten sponges. They examined, however, only one species of Pomacanthidae, a group shown to contain sponge-feeding species in the West Indies (Randall and Hartmann, 1967).

Among fishes there are several "cleaners" at Enewetak, those species which eat ectoparasites and consume mucus from the bodies of other, usually larger, fishes. Most important are members of the wrasse genus *Labroides*, particularly *L. dimidiatus*. There are also various invertebrate cleaners, usually shrimps, on Enewetak reefs.

Some fishes associate with invertebrates that are avoided by predators as one method of gaining protection. Anemonefishes associate with sea anemones; in spite of this, they are occasionally eaten by other fishes. Hiatt and Strasburg (1960) found a juvenile *Amphiprion melanopus* in *Apogon novemfasciatus*. Allen (1972a) reported that disoriented *Amphiprion* (due to "fin-clipping" manipulations) were sometimes eaten by groupers, particularly *Anyperodon leucogrammicus*. Allen (1972b) described a cardinalfish, *Siphamia fuscolineata*, sheltering among the venomous spines of the crown-of-thorns starfish, *Acanthaster planci*. Between eight and 31 fish were found with each of four *A. planci*; however, only a small percentage of starfish had the apogonid associated with it. Species of *Siphamia* are more often found associated with diadematid sea urchins.

A small group of fishes shelter among branched corals, some never leaving the coral. Hiatt and Strasburg (1960) illustrate some which include the gobies of *Gobiodon* and *Paragobiodon*, plus the scorpaenoid genus *Caracanthus*. There are similar invertebrate associates, particularly crabs of the genus *Trapezia* and some alpheid shrimps. A much greater number of fishes temporarily shelter in branched corals when danger threatens. The hundreds of *Chromis caerulea*, *C. atripectoralis*, *Dascyllus reticulatus*, and *D. aruanus* stationed above small heads of *Pocillopora* corals which can take nearly instant shelter on that head (Hobson and Chess, 1978) are astounding.

Hobson and Chess (1978) have examined the feeding relationship between zooplankton and planktivorous fishes of the lagoon margin. At their two study areas, one northeast of Jedrol within the strong influence of currents in the deep channel and the second in the lee of Bokandretok where currents are weak, they found that current patterns sharply affected trophic relationships. The plankters ingested by diurnal and nocturnal planktivores were quite different. There was an abundance of suitable zooplankton in strong current areas, whereas areas of weak currents were poor in zooplankton. These poor areas in the lee of reefs and islands were, however, rich in debris from the reefs and, among diurnal planktivores, many fishes here were adapted to feeding on algal fragments. Some species, common in both strong and weak current areas, showed a shift in diet between areas reflecting the type of food items in the water column.

Nocturnally, fish planktivores were more abundant in weak current areas feeding on larger zooplankton which is absent from the water column during the day. Much of this zooplankton shelters on or in the substrate during the day, rising into the water column at night. During the day many nocturnal planktivores shelter on reefs. Horch (1973) found both *Myripristis violaceus* and *M. pralinius* common in shallow water during the day, coexisting in coral caves of patch reefs and reefs fringing some islands. At night they left their shelters and often fed in mid-water within a meter of the water's surface.

Hobson and Chess (1978) found a clear-cut differentiation in the distance that various planktivorous reef fishes move away from reef shelter to feed in the water column. On windward lagoon margin patch reefs, they found that

species stationed farther from the reef had more cylindrical bodies with deeply incised caudal fins than species remaining relatively close.

The fish communities on lagoon margin patch reefs were examined in detail by Nolan (1975) for reefs between Enewetak and Medren. These reefs are typical of those found throughout the lagoon margin on the windward side. He divided the fish community into four assemblages:

1. The patch reef assemblage (about 25 species)
2. The roving fish assemblage (about 25 species)
3. The sand assemblage
4. The rubble assemblage (3 and 4 together about 50 species)

The most numerous fishes living on the patch reefs were cardinalfishes (Apogonidae) and damselfishes (Pomacentridae). A large percentage of these individuals are mid-water plankton feeders, relying on items brought by the steady cross reef flat currents from ocean to lagoon. Nolan (1975) found that fish species composition of lagoon margin patch reefs on the windward side visually censused at about 100-day intervals fluctuated considerably over 2½ years of observations. Among five "control reefs," each had 20 to 24 species at the end (mean 21). Individual reefs varied by as many as 10 species during the study. The numbers of individuals, however, varied by as much as a factor of 10 during the study. One reef went from about 100 individuals to 970 because of juvenile recruitment of two species of apogonids and pomacentrids. If increases related to juvenile recruitment were not considered (or in the case of those reefs where massive juvenile recruitment did not occur), numbers of individuals were much more consistent, varying by less than a factor of 2.

Nolan (1975) found considerable movement among reef fishes between lagoon margin patch reefs on the windward side of Enewetak. He reported various surgeonfishes, wrasses, and parrot fishes as ranging freely between reefs.

Although identifiable assemblages of fishes occur in a particular environment, there is small-scale variation in species composition. Nolan (1975) constructed artificial reefs, made of cement pipe "modules," on the lagoon margin between Enewetak and Medren to provide identical shelter to reef fishes which inhabited those reefs. Artificial reefs reached species equilibrium in 100 to 200 days, a figure equivalent to defaunated natural reefs, but the colonization pattern differed from natural reefs. About 10 species occurred on the artificial reefs (versus about 20 for small natural reefs), which had limited habitat diversity, and variation over time was much higher for artificial reefs than natural reefs.

Gladfelter et al. (1980) examined the fish communities of lagoon margin patch reefs between Enewetak and Medren and near the deep channel but utilized reefs over an order of magnitude larger than those studied by Nolan (1975), averaging 150 to 200 m^2 in area. Compared to western Atlantic patch reefs of similar size, Enewetak reefs are steeper sided with greater vertical relief and more complex surface topography. The number of species (visually censused) on the Enewetak patch reef varied between 76 and 109, with about 500 to 900 individuals per reef. Considering trophic categories, diurnal planktivores were more abundant on Enewetak than Virgin Island patch reefs, probably because of the consistent ocean to lagoon cross-reef currents. Herbivores were more diverse among Enewetak reefs with fewer individuals. The Virgin Islands reefs were surrounded by sea grass beds, a habitat lacking at Enewetak, and had more nocturnally foraging invertebrate-feeding fishes.

The interrelationships between reef fishes on Enewetak patch reefs are complex. Competition for space and food can be intense between species and among conspecifics. Factors controlling initial recruitment of juveniles and their eventual growth to adults are additional controllers of ultimate community composition. Nolan (1975) describes numerous instances of unique interactions among fish species inhabiting small patch reefs on the lagoon margin. Many of these interactions were the result of experimental manipulation, but others were simply the result of long-term careful observation of the environment. Nolan's (1975) record is, perhaps, the best such record of relationships and occurrences among a diverse group of fishes on small reefs over time.

Allen (1972a, b) described instances where removal of adult anemonefish from their host anemones was followed within a few weeks or months by recruitment of large numbers of juvenile *Amphiprion*. Anemones unoccupied by *Amphiprion* were not encountered by Allen (1972a, b), and he felt that anemone availability was one of the major factors limiting anemonefish populations at Enewetak. The situation has not changed since Allen's work; anemones remain relatively uncommon and *Amphiprion* populations are limited compared to other tropical Pacific areas.

The fish communities of the outer reefs, deep lagoon, and open ocean around Enewetak are not as well documented. Even the nearshore spur and groove is poorly known because of its normally hazardous surf conditions. The movement of herbivores and predators onto the reef flat with rising tides is well documented (Hiatt and Strasburg, 1960; and others). Population sizes, movement along the reef face, and foraging dynamics are not well known.

FISH REPRODUCTION AND RECRUITMENT

Most reef fishes reproduce by either laying demersal eggs on the substrate or releasing planktonic eggs in the water column. Both hatch as planktonic larvae. Larval life ranges from a minimum of 2 to 3 weeks to as much as 2 to 3 months. Lack of proper substrate for metamorphosis may greatly extend this time. Some information exists concerning the spawning habits of demersal- and planktonic-egged species at Enewetak.

Major families producing demersal eggs include pomacentrids, gobiids, and blennies. Swerdloff (1970) and Allen (1972a, 1975) have described various aspects of pomacentrid spawning at Enewetak.

Most of the larger fishes at Enewetak produce planktonic eggs. Relatively little has been published about the spawning of larger fishes at Enewetak. What has been written is limited to the papers by Helfrich and Allen (1975), Thresher (1982), and Bell and Colin (1986). There are considerable unpublished data of Colin and Bell. Spawning habits of about 60 species are known and, although general patterns are known for these, there are exceptions to every generalization.

Many planktonic-egged species can spawn at any time during the day in certain locations when tidal conditions are correct. This is generally true for the labrids and parrot fishes, but other families, such as the Pomacanthidae, are believed to spawn only near sunset (Thresher, 1982; Bell and Colin, 1986). In spite of the abundance of large piscivores, predation on spawning fishes appears to be rare. Predation on eggs immediately after release by particulate plankton-feeding fishes is also uncommon, occurring in only a few percent of spawning releases.

Planktonic eggs and larvae from both demersal and planktonic eggs are carried by currents during their development. Larvae produced on the windward side of the lagoon, particularly the northern part, would have an excellent chance of undergoing their entire development within the lagoon, since water residence times in that area are above the mean of about 30 days, reaching as much as 4 months. The mid-depth water return mechanisms of the lagoon would ensure return of larvae to the windward side in spite of the westward surface drift.

There is no distinct seasonality known in spawning of fishes at Enewetak, but relatively small differences cannot be ruled out. Gerber (1981) found approximately a two-fold increase in the mean number of fish eggs in mid-lagoon plankton tows during summer as opposed to winter periods, but considerable variability in individual collections indicated different means were not significant. Given the transitory nature of fish spawning, the observed patchiness of eggs is not surprising. A similar situation existed for fish larvae (Gerber, 1981). Higher concentrations of fish eggs and larvae at significant levels were found at Gerber's (1981) "behind reef" station than in the mid-lagoon during winter and may be the result of distance from sources (reefs and their immediate vicinity) of eggs and larvae. Other larvae are undoubtedly carried out to sea, but their potential fate is not well known. The presence of down-current eddies (in this case to the west) behind islands (and atolls) is well documented and may serve to return larvae to the vicinity of Enewetak after a period of days or weeks. More work is needed on this phenomenon. Many larvae are certainly lost into the general westward drift of the North Equatorial Current, but sufficient numbers of larvae develop within the lagoon or are returned by eddies to maintain fish populations at the atoll. A limited number of recruits must originate east of Enewetak, from Bikini and other atolls of the northern Marshalls, but in terms of numbers are probably overwhelmed by locally produced offspring.

Nearly all Enewetak fishes recruit as free-swimming larvae. Exceptions would include elasmobranchs (sharks, rays) bearing live young and a limited number of reef fishes which have live young (Brotulidae, Ophidiidae) or a greatly modified larval life (Syngnathidae). Most of the reef fishes have planktonic larvae which must make a transition when becoming juveniles, often moving into a reef environment crowded with others of their species and other species.

There was no significant evidence for seasonality of reef fish recruitment to artificial reefs in Nolan's (1975) study. Some species, however, did not recruit at all seasons. Possibly, this was because of the relative scarcity of those species, but one common species *Apogon "novaeguinae"* (the species identified as *novaeguinea* by Lachner, Schultz, and collaborators, 1953, appears to be *A. cyanosoma* though seemingly subspecifically different) did not recruit during the summer. Since it did appear in small numbers on natural reefs, Nolan (1975) attributed this, potentially, to reduced recruitment during the summer.

Year-round spawning activity and reproductive coloration were observed in some apogonids and pomacentrids. Female chaetodontids with ripe ovaries were noted at all seasons by E. S. Reese (personal communication).

The role of predators in limiting the numbers of some small reef fishes on patch reefs has been amply demonstrated by Nolan (1975). He found that when additional pomacentrids (*Chromis* and *Dascyllus*) were added to reefs already at saturation levels with conspecifics, the new arrivals were readily eaten by cruising piscivores. One artificial reef already at equilibrium had additional damselfishes added. Within a day or two almost all additions had perished. Shelter is a factor which limits absolute numbers of such reef fishes; the excess individuals which cannot find a refuge are easily taken by the abundant predators of Enewetak reefs.

CIGUATERA

Ciguatera is the most common tropical fish poisoning known in the Marshall Islands, including Enewetak. Randall (1980) has reviewed the historical reports of ciguatera in the Marshall Islands. Of relevance was information provided by Iroij Johannes Peter that before 1946, some reef fishes from certain areas of Enewetak were poisonous to eat. Randall (1980) described instances of ciguatera poisoning at Enewetak. The internal organs (which are considerably more toxic than the flesh) of 47 species of large reef fishes were tested using a mongoose bioassay for toxicity. At least one individual of five species produced the strongest reaction (death within 48 hours), whereas 31 species produced at least some response by mongooses to ingestion. Even in the species producing the most frequent reaction, the percentage of individuals producing a response is relatively small. Ciguatoxic fishes at Enewetak were found to fit the recognized pattern of being generally large individuals, mostly roving predators, and largely piscivorous (Randall, 1980). No evidence exists that the occurrence of

ciguatera at Enewetak is related to radiation in the environment. Disturbance of the marine environment (dredging, construction, wrecks, etc.) has been strongly implicated in producing ciguatera (Randall, 1980).

The probable causative organism of ciguatera, a dinoflagellate *Gambierdiscus toxicus*, has been identified and the toxin collected and purified.

Sharks

Several species of sharks are common at Enewetak. They range from nearly harmless to extremely dangerous. Some are found in only one environment, whereas others are nearly ubiquitous.

The blacktip reef shark, *Carcharhinus melanopterus*, is abundant on the reef flats all around Enewetak. Hiatt and Strasburg (1960) reported *C. melanopterus* was the most common shark on windward and leeward reefs. Hobson (1963) reported blacktip sharks were most often observed on sand and coral rubble flats in shallow water. It often penetrates into water so shallow the dorsal fin and back are well exposed. Small *C. melanopterus* individuals are most common on the reef flat. Larger individuals cruise the spur and groove zone offshore and are often seen around lagoon margin pinnacles.

The whitetip reef shark, *Triaenodon obesus*, is perhaps the next most commonly seen species. It is most abundant in the lagoon along the marginal sandy areas and reefs but is also found on seaward reefs. Hobson (1963) found *T. obesus* most often on patch reefs and coral ledges around the margin of the lagoon. Randall (1977) reported that *T. obesus* feeds largely on reef fishes, especially scarids and acanthurids, plus octopuses.

Also found in the lagoon is the lemon shark, *Negaprion brevirostris*, which although large, penetrates into relatively shallow water. The author once nearly stepped down onto the back of a 1.5 m lemon shark while wading ashore on Ikuren in knee-deep water.

The most studied and the most dangerous shark at Enewetak is the gray reef shark, *Carcharhinus amblyrhynchos*. It is found throughout the lagoon and on the seaward reefs. Hobson (1963) felt it was most abundant in the deeper waters of the lagoon and passes. Attacks on humans are discussed subsequently. Johnson and Nelson (1973) described in detail the threat display of the gray reef shark, which often precedes an attack. Sharks placed in a situation of a diver potentially restricting its escape produced the most intense displays: an exaggerated, often rolling, swimming motion with back arched, pectoral fins dropped, and snout lifted. Starck (MPRL, 1971 to 1972) elicited attack responses on a small wet submersible by pursuing *C. amblyrhynchos*. A more detailed account is presented in Anderson (1980). Subsequently, this attack and its preceding threat display have been investigated by Nelson (MPRL, 1978, 1979). He found that the shark usually attacks after displaying if the object or person continues to approach. The attacks are sudden, high-speed strikes, often with the mouth open. He believed that "oriented pursuit" by the small submarine was of primary importance in releasing an attack. A straight-line pass near the shark never released an attack, although it did produce the threat display. For more information on gray reef shark behavior, see Nelson et al. (1986).

Randall (1980) reported that *C. amblyrhynchos* from Enewetak and other localities fed mostly on reef fishes and, to a lesser extent, on cephalopods. It is the most common shark seen on seaward reefs. Off the southwest islands and on the leeward reef face, it usually appears before the silvertip shark, *C. albimarginatus*, and outnumbers the latter shark two or three to one. In the lagoon it is common around mid-lagoon pinnacles where it seems particularly aggressive. Often when a boat stops in mid-lagoon on a calm day, one or more *C. amblyrhynchos* will rise to investigate the boat from water 50 to 60 m deep.

The movements of *C. amblyrhynchos* tagged with ultrasonic transmitters have been investigated by Nelson (MPRL, 1978, 1979). He has determined that gray reef sharks often move surprisingly long distances around Enewetak. Deep-water gray reef sharks tagged on or near the drop-off of the seaward reefs ranged as much as 16 km along the reef in one night. They were not as predictably home ranging as lagoon gray reef sharks, and Nelson (MPRL, 1979) suggested they might represent a more nomadic segment of the population. Lagoon grays were tracked for as long as 21 days, and although some stayed in one area, others moved considerably. One individual tagged at the mid-lagoon "dome" pinnacle spent the daylight hours near that pinnacle but ranged widely at night. Its home range was estimated at about 53 km^2. McKibben and Nelson (1986) discussed movements of tagged gray reef sharks at Enewetak.

Other seaward reef sharks are the silvertip shark, *Carcharhinus albimarginatus*, and Galapagos shark, *C. galapagensis*. The silvertip shark is found normally on seaward slopes below 20 to 30 m, although Randall (1980) observed one individual in the lagoon in water 2 m deep. There are reports of *C. albimarginatus* as deep as 400 m (Randall, 1980). Silvertip sharks feed almost exclusively on fishes, both reef and open water. Randall (1980) also found at Enewetak a gray reef shark over 60 cm in total length in the stomach of a *C. albimarginatus* that was 1.6 m in total length. The Galapagos shark is a large, dangerous species, but fortunately it is uncommon at Enewetak. Randall (1980) collected only a single specimen, but little is known of its habits beyond feeding on fishes (including sharks) and cephalopods.

Probably the largest dangerous shark in Enewetak waters is the tiger shark, *Galecerdo cuvier*. Randall (1980) examined two specimens from Enewetak, 1.7 and 2.4 m precaudal length (length minus the caudal fin), of 72 and 174 kg, respectively. McNair (1975), an accurate and experienced shark observer, while diving on the leeward seaward reef, observed a huge tiger shark pass above him

which he estimated was longer than the 21-ft boat it passed by. Tiger sharks are seldom seen by divers and, therefore, are not as much of a hazard as some smaller, dangerous species. Randall (1980) found the scutes of a green turtle shell, shark vertebrae, bird feathers, digested shark fins, and pieces of a porpoise in the stomachs of Enewetak *G. cuvier*.

There have been several instances of shark attacks at Enewetak. Most have involved the gray reef shark and, in some, injury occurred to the human involved. Hobson et al. (1961) documented two incidents with gray reef sharks in which spearfishing probably stimulated aggressive behavior. Fortunately neither instance resulted in injuries. Not so lucky was another individual whose head was slashed by the upper jaw of *C. amblyrhynchos* after the powerhead he was using to try to kill this shark failed to detonate on impact (Randall, 1980).

In April 1978, another attack by *C. amblyrhynchos* occurred in which a 1.5-m (5-ft) long individual severely mauled the right arm of a diver and attacked his diving partner (M. V. deGruy and P. Light, unpublished report). In this case deGruy approached the shark, which was exhibiting the threat posture, in an attempt to photograph it. When deGruy triggered the electronic strobe of his camera, the shark turned, rushed toward deGruy, and seized his arm. Seconds later the shark tore a chunk from one diving fin. As the diver's companion, Light, swam to his assistance, the shark bolted toward Light and badly slashed his hand. The shark disappeared. Both divers subsequently recovered from their wounds.

The most recent attack by *C. amblyrhynchos* on humans occurred in January 1982 when one of the repatriated Marshallese, while spearfishing, had his left arm mauled by what was probably a gray reef shark. Several sharks were around this fisherman and his two companions, who were carrying a considerable quantity of dead fishes.

Randall and Helfman (1973) reported two instances of *C. melanopterus* menacing humans at Enewetak.

It is interesting to note that despite repeated success in producing threat displays and attacks by *C. amblyrhynchos* by pursuit with small wet submersibles, similar attempts have failed to produce the threat or attack by *C. albimarginatus*, *C. melanopterus*, and *T. obesus* (Nelson, MPRL, 1979; Starck, MPRL, 1971 to 1972).

Crater Life

Nolan et al. (1975) described bottom substrata and fishes inhabiting the two small craters (Cactus and Lacrosse) at the north end of Runit Island. Hard substrata were restricted to the upper 4 m and the sides of both craters sloped quickly to a sediment plain at about 12 m deep. The bottoms of the craters were "heavily excavated by several species of gobies and burrowing shrimps." Other bioturbating organisms were also present. Colonies of *Halimeda* and *Derbesia minima* were abundant on the sediment bottom. Hillis-Colinvaux (1980) found no Halimedae in Lacrosse crater but found a pure, dense strand of *Halimeda incrassata* in the murky center of Cactus crater at 11 m depth. This merged peripherally with *Caulerpa ad serrulata*, but no loose plants were seen on the sides of the crater. *Halimeda incrassata* was rare at Enewetak (Hillis-Colinvaux, 1980), and the Cactus crater population was the only dense (about 200 or more thalli m^{-2}) strand found at Enewetak. Hillis-Colinvaux (1980) suggested that the extremely soft and fine sediment of Cactus crater might have promoted the growth of this dense strand, possibly from a limited number of vegetative propagules.

Nolan et al. (1975) found little living coral in the Runit craters but reported that "molluscs, crustaceans, polychaetes, zooplankton, algae, and phytoplankton found in the craters seemed typical of the fauna and flora occurring in the adjacent lagoon or upon the reef flat." Eighty-four species of fish were observed or collected in the craters; the number is incomplete for various cryptic families. Censuses at near high and low tides indicate fewer individuals of species at low tides than at high tides.

The third small atomic test crater, Seminole, on Boken (North) Island has not been examined biologically. Adjacent sand flats seem to be an area with high numbers of small blacktip sharks. Circulation into Seminole crater is much more restricted than circulation into either Runit atomic crater.

The three large thermonuclear craters in the north lagoon have not previously been described biologically. During the Enewetak Submersible Project, several dives were made in Oak crater using the submarine, and additional scuba dives were made on the crater slope. The level bottom of Oak crater (Ristvet et al., 1978; Chapter 4, this volume) was heavily bioturbated, almost certainly by callianassids, with a mound density equaling that observed anywhere else at Enewetak. In addition, the irregular urchin *Maretia planulata* occurred in high densities of 10 m^{-2} on the surface of sediment at the bottom of the crater. Similar bioturbation was evident in Koa crater, although at a lesser depth. Nelson and Noshkin (1973) did not consider that biologically mediated presentation of radionuclides from within the sediment column to the water column was occurring in Koa (and Mike) craters but that the "principal loss of activity from the deposits may only be from the slow release to the overlying waters."

Smith and Brock (MPRL, 1976) found that the Mike-Koa and Oak craters have large amounts of rubble in the vicinity of the craters which provide an unfavorable substratum for coral growth. The locations of the craters are described in Chapter 3 of this volume.

Why Are There No Sea Grasses at Enewetak?

Tsuda et al. (1977) have summarized the known distribution of sea grasses in Micronesia. Only one species, *Thalassia hemprichii*, is known from the Marshall Islands. Records exist for it from Ailinglapalap, Jaluit, and Ujilang

Atolls. At the last atoll, Fosburg (1955) reported "a rather extensive strip" of *T. hemprichii* along the lagoon shore of Ujilang Island.

Thalassia hemprichii was found by the author only along the lagoon shore of Ujilang Island in July 1982. None was seen on several lagoon shores on the windward side visited or on two coral pinnacles with extensive sandy areas above 15 to 20 m depth. The strip along Ujilang Island occurred only at depths <1 m. Reliable information exists that *T. hemprichii* (or any other sea grass) does not occur at Bikini, Rongelap, or Rongerik (Emery et al., 1954). Fosburg (1955) reported on visits to many north Marshall atolls (Kwajalein, Lae, Ujae, Wotho, Likiep, Aihik, Bikar, Pokak, and Ujilang) with Ujilang the only of these where sea grasses were noted. At Kwajalein, significant diving and collecting activities by knowledgeable marine biologists over large portions of the atoll have failed to reveal *T. hemprichii*. Tsuda (Chapter 1, Volume II) documents that no record of sea grasses from Enewetak exists. Because of the large amount of marine work carried out at this atoll, it is reasonable to say they do not occur here.

The presence of *T. hemprichii* at Ujilang, only 200 km away, is intriguing. The decline, however, in the numbers of sea grass species eastward through Micronesia (Tsuda et al., 1977) and the probable absence of *T. hemprichii* at most—if not all—other Marshall atolls, indicate that perhaps there has been no opportunity for transport of *T. hemprichii* to Enewetak. The areas upcurrent of the atoll are similar atolls without sea grasses. A similar condition has been noted for *Sargassum* (Tsuda, 1976) with no records from any northern Marshall atoll, including Enewetak. The means of dispersal of *T. hemprichii* are limited. Potentially it could be transported as drift material torn loose during storms or as drifting seeds or seed capsules. Both potential mechanisms are current dependent, which would work against transport to Enewetak. Atolls farther south, in the influence of the Equatorial Countercurrent, may have received their populations via this current.

Why Are There No Mangroves at Enewetak?

Wiens (1962) has summarized much of the information on mangroves on atolls. He cites records of "mangroves" on several southern Marshall Island atolls. Hatheway (1953) described stands of *Sonneratia caseolaris* and *Bruguiera conjugata* on Arno Atoll. Wiens (1956) observed a tidal inlet on Ailinglapalap Atoll with three species of mangroves. Fosburg (1955) reports *B. conjugata* on Utirik, Ailuk, and Lae to be rare and limited to "wet depressions." Otherwise, he does not record any "mangrove" species, particularly those of the Rhizophoridae from the northern Marshall Islands.

Again the situation is similar to sea grasses. Mangroves can certainly survive at atolls like Enewetak, but it is likely their transport mechanisms have never allowed their introduction.

Zoogeographic Considerations

One interesting phenomenon is that many marine animals that are relatively scarce at Enewetak are much more common elsewhere. This seems true even within the Marshall Islands where disparity exists between Enewetak and the more southerly Marshall Island atolls—such as Kwajalein, Majuro, and Arno—which have had a significant collecting effort.

This scarcity is true among fishes. For example, Allen (1972a) commented that most anemone species were relatively scarce at Enewetak as compared to his personal observations in Tahiti and literature from the Nicobor Islands. "Several hours of intensive searching may at best result in finding four or five widely scattered specimens (of anemones) of the variety which harbor *Amphiprion*." As has been pointed out elsewhere, even when present, the occurrence of anemones may be transitory.

Hiatt and Strasburg (1960) indicate that a number of fish species are uncommon or rare at Enewetak (and often Bikini) compared to Arno Atoll. They felt that Arno was a more productive atoll than either Enewetak or Bikini because it is located in an area of upwelling where the North Equatorial Current and Equatorial Countercurrent meet and because it has a higher rainfall than the other two atolls. Whether this has an effect on the abundance of reef fishes or whether the differences observed are produced by sources of larval recruits, etc., is not known. Species of *Plesiops* and *Pseudogramma* are among fishes that are less common at Enewetak. Randall (1986) lists a number of species from Kwajalein Atoll which, in spite of comparable collecting effort, are not known from Enewetak.

Within the overall picture of Indo-West Pacific shore fish distribution, the Enewetak fauna is less diverse than the "core" areas of the Indo-Malayan Archipelago. This is well known for individual families (Allen, 1975), but the Enewetak fish fauna is at a level of diversity "expected" when compared to adjacent areas. The differences exist with respect to abundance of quite a number of species.

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Chapter 8

*Intertidal Ecology of Enewetak Atoll**

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INTRODUCTION: THE INTERTIDAL ENVIRONMENT

At an atoll, land and sea meet at a precarious, dynamic interface that often bears evidence of horizontal and vertical movements over past centuries and millennia. In the shorter-term dynamics of ecological time, the intertidal region of an atoll exposes the plants and animals that would earn their livelihood there to a particularly severe physical environment.

The vertical tide range on the shores of small oceanic islands is narrow. At Enewetak, it averages 0.8 m, and the spring tide range is 1.2 m. Over the 18-year period 1952 to 1969, the highest recorded tide was +1.8 m and the lowest was −0.1 m, relative to prior lowest low water. Despite this small range, many events within the intertidal region differ markedly from those occurring below datum and supratidally. Few marine organisms can tolerate the supratidal fringe, wetted only by rain and sea spray and subject to intense heat for long periods. Here physical factors profoundly affect the nature of the substrate. Within the intertidal zone, conditions are less severe but still stringent; substrate temperatures commonly reach 38°C (Wiebe, Johannes, and Webb, 1975). Dissolution of limestone reef rock substrate by rain and biological destruction by boring organisms are important processes (Tracey and Ladd, 1974). All intertidal habitats are subject to strong insolation and rain at low tide, and windward intertidal environments bear the brunt of heavy wave action at high tide. At the reef rim, coralline algae grow and accumulate calcium carbonate rapidly. Their growth also cements detritus and rubble into reef rock (Smith and Harrison, 1977; Tracey and Ladd, 1974).

This chapter summarizes the present state of knowledge of the ecology of intertidal environments at Enewetak. It emphasizes the windward, seaward reef platforms for several reasons:

1. They have been the most thoroughly studied, both geologically and at several trophic levels of the ecosystem.
2. They represent a habitat type of widespread occurrence throughout the tropical Indo-West Pacific (IWP) region on both oceanic and continental islands and on continental shores (Kohn, 1971); data from Enewetak thus provide a basis for comparisons with other IWP areas.
3. They afford significant comparisons and contrasts with adjacent subtidal coral reef habitats; in contrast to such reefs they are physically harsh rather than equable, and their topography is simple rather than complex (Kohn, 1971).

In their pioneering study of the Enewetak coral reef community, Odum and Odum (1955) characterized the basic pattern of six physiographic zones comprising the windward interisland reef 0.4 km north of Japtan (Muti) Island, from the seaward edge toward the lagoon:

1. *Windward buttress zone.* Spur-and-groove or surge channel-and-buttress zone, just seaward of the highest part of the platform, the coral–algal ridge. This is the upper portion of the inaccessible *mare incognitum* (Smith and Harrison, 1977).
2. *Coral–algal ridge.* "A low, narrow ill-defined strip of limestone about 50 feet (16 m) wide" (Odum and Odum, 1955). Soft, fleshy algae (such as *Dictyosphaeria intermedia, Lobophora variegata, Ceramium, Dictyota,* and *Caulerpa elongata*) cover the irregular surface, and the crustose coralline alga *Porolithon* occurs in small patches. Small clumps of corals *(Acropora palmerae, Pocillopora, Millepora platyphylla)* occur in protected sites. Algal ridges are more extensive on island than interisland reefs.
3. *Encrusting zone.* "The first 200 ft (66 m) downstream from the ridge is a high, gently sloping plateau that at low spring tide is covered with only 6 in. (115 cm) of water. It is relatively the smoothest area with corals being either of a flat encrusting growth form or restricted to low rounded 'heads' but little raised above the general reef surface. The range between tops of heads and

*This chapter is dedicated to the memory of the late Paul J. Leviten.

ridges and the bottoms of depressions is only about 1 ft (30 cm). As on the coral–algal ridge zone, sheets of yellow *Acropora* and *Millepora* are conspicuous. In addition there are scattered low, rounded heads of *Porites lobata* and several species of faviids. ...living coral colonies on these low heads are often crescent or doughnut shaped probably because the higher center portions are killed periodically by exposure during exceptionally low spring tides. Filamentous red, brown, green, and blue-green algae form heavy encrusting mats over all of the zone which is not covered by coral, there being no areas of white sand as in the back reef zones. Small sea anemones are abundant, occurring in clusters throughout the algal mat. ...Coral cover is much less than half the surface area. ...The zone receives pulses of foam-water as the breakers throw rolls of water up on the plateau. Since there is a distinct slope the current is always strong even at low spring tide when the water pours steadily across like a broad mountain stream rippling over a rocky bed" (Odum and Odum, 1955).

4. *Zone of smaller heads*, 5. *Zone of larger heads*, and 6. *Zone of sand and shingle* are the lagoonward zones distinguished by Odum and Odum (1955). They are completely subtidal and will not be further discussed here.

The following description of a windward reef platform adjacent to an island is taken from Leviten and Kohn (1980). The platform on the windward (east) side of Enewetak Island (Fig. 1) is about 90 to 120 m wide, "and mainly topographically simple or smooth, but certain portions have numerous holes and depressions. Wave action is extremely heavy and constant on the seaward bench margin at high tide, but is damped somewhat on the inner portions by an extensive low coralline algal ridge on the seaward margin." At Sta. F7 of Leviten and Kohn (1980), "the inner 20 m is scalloped and pitted reef rock undergoing chemical dissolution (Revelle and Emery, 1957). It lacks macroscopic algal cover, but in certain areas bears a thin, slippery film of blue-green algae *[Calothrix crustacea]*. ...An incipient algal turf begins ≃25 m from shore and increases in luxuriance in a seaward direction. ...A shallow swale, unique to this bench among those studied, occurs between 50 and 65 m from shore. This area is covered by several centimeters of water even during low tide and harbors a healthy 2-cm-thick algal turf. ...The bench is pitted and dissected between 65 and 80 m from shore. Algal cover is thick, and algal species richness is higher than on other portions of the bench. ...The *Porolithon* ridge is evident ~80 m from shore and continues to the seaward margin of the bench ~100 m from shore, where it is dissected by numerous small surge channels and grooves. The ridge has a scoured aspect, possibly due to intense grazing activity by herbivorous fishes at high tide, and lacks an extensive fleshy algal cover, save for a film of blue-green algae."

In order to characterize the microhabitats of benthic invertebrates more precisely, bench substrates are classified as shown in Table 1 (see also Leviten and Kohn, 1980).

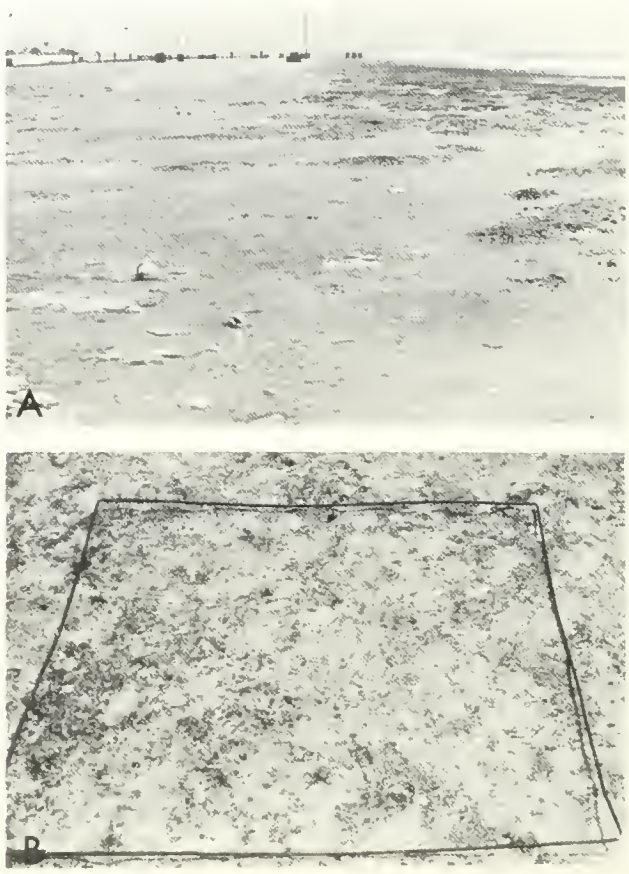

Fig. 1 The windward platform of Enewetak Island. a, looking NE at a neap low tide, April, 1979; b, a 1-m^2 quadrat on the same area shown in a, indicating the smooth topography of the substrate.

Temperatures recorded by Havens (1974) on intertidal substratum exposed to air reach 36.5°C on exposed reef rock on the windward reef platform, 38.5°C on bench rock, and 39°C on rubble-covered beaches. The maximum temperature recorded under rocks and in holes was only 32.5°C. Water temperatures in tidal pools reach 38°C, in contrast to submerged reefs, which do not exceed 32°C.

GEOLOGICAL PERSPECTIVE

Shallow-water marine environments at Enewetak extend back in time 50,000,000 years. A vertical borehole drilled in 1952 (Ladd and Schlanger, 1960) reached volcanic bedrock after traversing 1300 m of calcareous material derived solely from shallow reef-building and reef-associated organisms. Fossils in the reef limestone just above the discontinuity were of Eocene age, indicating a long-term average subsidence rate of about 0.03 mm yr^{-1} (Menard, 1964). Recovery of land mollusc fossils from core samples indicates that, during probably cooler parts of the Neogene, Enewetak stood higher above sea level than at the present time (Ladd, 1958).

TABLE 1

Classification of Windward Reef Platform Substrates

Sand
Extensive sand patches
Sand in depressions in reef limestone
Sand under coral rock
Coral rubble with or without sand
On flat bench surface
In depression on bench
Very thin layer of sand on bench
On flat bench surface
In depression on bench
Limestone bench bare of sand or algal turf
Smooth
Rough
In depression
Bare beachrock
Algal turf on reef limestone bench, typically binding sand
On smooth bench surface
On rough bench surface
In depression on bench surface
Dead coral boulder
Crustose coralline algae

The Quaternary record shows "at least four stratigraphic intervals representing reef growth and associated lagoonal sedimentation during relatively brief periods of Quaternary interglacial high sea levels, overlying unconformities representing periods of emergence and weathering during glacial lowering of sea level" (Tracey and Ladd, 1974). The uppermost unconformity, about 10 m below present sea level, separates sedimentary rocks less than 6000 years old from sediments about 120,000 years old. The limestone rock pavement constituting the present extensive windward reef platform adjacent to Enewetak Island (Fig. 2) is about 4000 years old and is a currently developing unconformity (Tracey and Ladd, 1974; Buddemeier, Smith, and Kinzie, 1975). The latter authors characterized the rock at and near the seaward algal ridge crest as well lithified "poorly sorted coral rubble, coarse sand, and obvious (?) coralline algae in a fine-grained calcareous matrix." The composition of this material suggests that it was formed in a subtidal, sedimenting environment very different from that at the site today. Geological and radiocarbon studies of this material suggest the following temporal scenario of the interplay of sea level changes and biotic activities during the Holocene, leading to the intertidal environments of Enewetak at the present cross section of time: The sea was less than 3 m below its present level 6000 years ago (ybp), rising to a maximum 3500 to 2000 ybp, a period of rapid reef growth. At 4000 ybp, the age of the present surface rock when the corals shown in Fig. 2 were living, sea level was probably about 0.3 m higher than at present. From 2000 to 1000 ybp, emergence and extensive surficial erosion of the reef accompanied a drop in sea level to its present level.

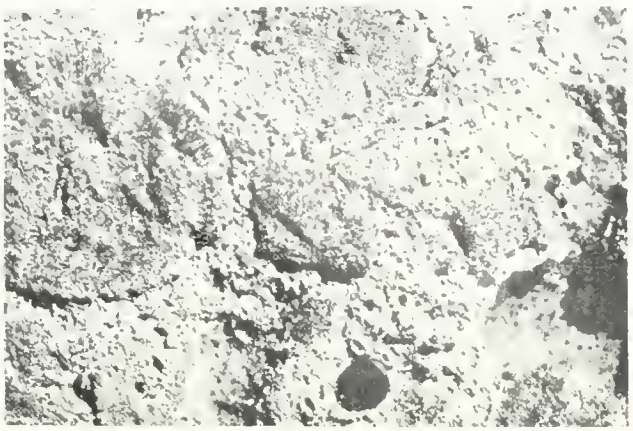

Fig. 2 Reef limestone surface in the inshore 20 m of the windward platform at Enewetak Island, showing corals in growth position and the effects of subaerial, marine, and biogenic erosion. The present level of the rock is too high in the intertidal zone for coral growth. Dark spots in small higher pits and in the pothole at lower right are limpets, *Siphonaria normalis*. The lens cap is 52 mm in diameter.

Shorter-term geochemical processes have been elucidated in studies of calcification rates to be discussed below. They show that the interisland windward reef platform is accreting vertically at a rate of about 3 mm yr^{-1} (4 kg m^{-2} yr^{-1}) in the absence of sea level change (Smith, 1973). If most of the products of calcification were retained on the platform during the 1952 to 1970 period in which there was no net sea level change, an estimated shoaling of 5 cm would have occurred; if most net products of calcification were lost by transport to the lagoon, no net change in platform level would have occurred.

Calcification rates subtidally on the windward reef slope are somewhat lower, about 1 to 2 kg m^{-2} yr^{-1} in the buttress or spur-and-groove zone, but 3 to 6 kg m^{-2} yr^{-1} where coral cover is virtually total at depths of 15 to 25 m (Smith and Harrison, 1977).

BIOLOGICAL PATTERNS AND PROCESSES

Primary Productivity

The intertidal and shallow subtidal windward reef platforms at Enewetak are highly productive, particularly where covered by a dense algal turf. The mainly subtidal interisland reef north of Muti Island, close to the site of the original study by Odum and Odum (1955) has been the most intensively studied. Smith and Marsh (1973) measured primary productivity along two transects normal to the seaward reef edge by two independent methods—rate of oxygen production and rate of carbon dioxide fixation—which gave results in close agreement. At Transect II (tr II; 340 m), the red crustose coralline alga *Porolithon onkodes* and the brown alga *Lobophora varie-*

gata were the dominant cover organisms of the algal ridge, and corals were very sparse. For about 160 m lagoonward, *Porolithon* and the turfy red coralline alga *Jania capillacea* dominated; some zoanthids and holothurians were also common. Over the next 180 m, the corals *Porites*, *Acropora*, and *Heliopora* increased in abundance on the limestone pavement, and *Porolithon* continued. Transect III (tr III; 270 m) was characterized by cover of *Porolithon* at the algal ridge and *Jania* turf throughout. Foraminifera and gastropod molluscs were common, but there were virtually no corals on the transect. Water depth over these transects at low tide was less than 1 m.

As Table 2 indicates, the transect with the greater dominance of algae throughout (tr III) was the more productive. And as shown in Table 3, only the predominantly algal turf areas were highly autotrophic; the other regions produced about as much organic matter as they consumed. Smith and Marsh (1973) also demonstrated that the $C:O_2$ metabolic quotient for the platform was very close to 1.0, as prior authors had assumed but had not tested.

TABLE 2

Gross and Net Primary Organic Productivity of an Interisland Windward Reef Platform at Enewetak Atoll*

	Daytime gross productivity	Daytime net productivity
Transect II	0.50	0.25
	2690	1345
Transect III	0.97	0.72
	4249	3154
Algal ridge	0.14	0.11
	550	240

*Data from Smith and Marsh (1973) and Marsh (1970). Upper figures: g C m^{-2} h^{-1}; lower figures: g C $m^{-2}y^{-1}$

Primary productivity of algal ridge crest areas dominated by *Porolithon* is much lower than the transect as a whole (Tables 2 and 3). Marsh (1970) concluded that this zone contributes much less to overall reef productivity than the others and that the reef-building activities of the crustose coralline algae are more important than their energy fixing.

Bakus (1967) estimated net primary productivity of the inner portion of the Enewetak Island platform where the blue-green algae *Calothrix crustacea* and *Schizothrix calcicola* are the dominant plants. Because his method measured increased standing crop in cages that excluded large herbivorous fishes but not small fishes or benthic invertebrates, the result, about 440 g C m^{-2} yr^{-1}, is undoubtedly an underestimate.

Nutrient Cycling

Because nitrogen in forms assimilable by photosynthetic organisms is an important limiting factor of primary productivity in the sea, the recent discovery that nitrogen fixation occurs at high levels on Enewetak's windward reef platforms (Webb and Wiebe, 1975; Webb, DuPaul, Wiebe, Sottile, and Johannes, 1975) is an important contribution to understanding coral reef-associated ecosystems. Studies at tr II and tr III described above indicated increasing concentrations of nitrate and ammonium as water crosses an island reef platform. The highest rates of production (about 1.5 nmoles cm^{-2} h^{-1} each of NO_3^- and NH_4^+) occurred on rock surfaces supporting a mixed algal turf dominated by *Calothrix crustacea* (about 80%) and *Schizothrix calcicola* (about 20%). This rate of nitrogen fixation is comparable to those in managed agriculture (Wiebe, Johannes, and Webb, 1975). *Calothrix* covered the surface as a thin, yellow-brown film over large areas of the platform and penetrated the limestone to a depth of several millimeters (Webb and Wiebe, 1975). Although the nitrogen fixing, chemoautotrophic bacterium *Nitrobacter agilis* colonized slides placed on the substratum and after 4 weeks attained densities high enough to fix NO_3^- at the observed rates

TABLE 3

Ratio of Productivity and Respiration on an Interisland Windward Reef Platform at Enewetak Atoll

Habitat type	Daytime net* productivity	Nighttime* respiration	Daytime gross* productivity	24-hour gross P:R	Reference
Coral–algal	0.4	0.4	0.8	1.0	Odum and Odum, 1955
Coral–algal (Tr II)	0.25	0.25	0.5	1.0	Smith and Marsh, 1973
Algal (Tr III)	0.72	0.25	0.97	1.9	Smith and Marsh, 1973
Algal ridge	0.11	0.04	0.14	1.8	Marsh, 1970

*g C m^{-2} h^{-1}

(Webb and Wiebe, 1975), Wiebe, Johannes, and Webb (1975) concluded that *Calothrix* is the most abundant and important nitrogen-fixing organism. It is extremely tolerant of the high range of temperatures and salinities characterizing its environment. Under experimental conditions, rates of N fixation doubled between 27°C and 36°C; the limiting temperatures were 24°C and 39°C. Experimental salinities between 3% and 45% did not affect fixation rates (Wiebe, Johannes, and Webb, 1975).

Predominantly algal reef flats are thus extremely important as a source of fixed nitrogen for adjacent communities and hence a critical source of their high productivity. Wiebe, Johannes, and Webb (1975) concluded that fixed nitrogen enters the rest of the reef ecosystem via three routes: (1) herbivorous parrot fishes and surgeonfishes that graze on *Calothrix crustacea* have low assimilation efficiency, and much of the organic matter in their food is liberated as feces; (2) *Calothrix* growing in the surf zone is broken off the substrate and moved downstream by lagoonward currents, where it is more subject to herbivory; "benthic algal fragments constituted by far the largest portion of the net plankton on the windward interisland reef at Enewetak, and *Calothrix* constituted 20 to 60% (by volume) of these fragments" (Wiebe, Johannes, and Webb, 1975); (3) *Calothrix* may release much of its fixed nitrogen into solution; in culture as much as 40 to 60% was released as peptides and amino acids.

Concentration of reactive and organic phosphorus does not change as water passes over tr II; at tr III, reactive P decreased and organic P increased in concentration, both slightly but consistently (Pilson and Betzer, 1973). Samples of reef rock dominated by *Schizothrix* actively take up phosphorus at a mean rate of 0.27 nmole P cm^{-2} h^{-1} during the day but also continually lose labeled P; mats dominated by *Jania* showed very little net uptake or loss (Pomeroy, Pilson, and Wiebe, 1974). These authors did not detect any special mechanism for retention of phosphorus by the windward reef platform community. Phosphorus incorporated by *Schizothrix* may be cycled through the food web by herbivorous fishes and invertebrates, which excrete it as phosphate.

Calcium Transport and Calcification

In addition to monitoring organic carbon production, Smith (1973) was able to use the CO_2 system of the interisland windward reef platform to determine gross calcification rates. Both a transect dominated by algae (tr II) and one with both algae and corals (tr III) added $CaCO_3$ at a rate of about 4 kg m^{-2} yr^{-1}, comparable to similar habitats elsewhere (Smith and Kinsey, 1976). Smith (1973) estimated the erosion rate at less than 1 kg m^{-2} yr^{-1}, sufficiently close to the standard error of the calcification rate to be ignored. Net calcification on the interisland reef platform thus probably approximates gross calcification. Locally production may be much more rapid: coralline algal pavement at the reef rim produces $CaCO_3$ at a rate of 8 to 16 kg m^{-2} yr^{-1} (Smith and Harrison, 1977).

Bacteria

DiSalvo (1973) noted the occurrence of a reduced layer of sand, suggesting bacterial decay of plant material, at the foot of beaches on the windward sides of Enewetak and Parry Islands.

Benthic Flora

Studies of the algae of the windward platforms subsequent to the initial work of Odum and Odum (1955) have noted some differences but have been neither thorough nor frequent enough to determine whether they indicate spatial or temporal patchiness, or both, or long-term trends. At the algal ridge crest and for about 200 m lagoonward on interisland platforms, the crustose *Porolithon onkodes* and the turf-forming *Jania capillacea* continue to dominate the surface of the lithified reef rock described above (Buddemeier, Smith, and Kinzie, 1975). Bailey-Brock, White, and Ward (1980) characterized four macroalgal zones inshore of the algal ridge crest on the island reef platform at Enewetak Island (Table 4) where turf-forming algae dominate. The algal turf is much thicker—about eight times as much biomass—and holds much more water at low tide in their zones 3 and 4 than in the inshore zones. Such turfs are the characteristic algal growth form in physically stressed tropical environments. They are more resistant to desiccation at low tide and to herbivory than separate individual plants, which are more productive and better competitors but are less resistant to harsh physical conditions (Hay, 1981).

The importance of the widespread blue-green alga *Calothrix crustacea* has been mentioned above. This diaphanous, yellow-brown film covers large areas of the windward flat. "Along the upper intertidal bench zone another growth form of the same species occurs as a black, feltlike mat up to 5 mm thick. At low tide, most of this mat dries out. It is not heavily grazed by fish owing to the shallowness of the water in which it grows. In areas of the windward reef flat, dominated by other algae, *C. crustacea* is found ubiquitously as an epiphyte" (Wiebe, Johannes, and Webb, 1975).

In their initial study, Odum and Odum (1955) distinguished several ecological groups of primary producers in the intertidal region of the interisland transect: phytoplankton; zooxanthellae in coral polyps, sea anemones, and *Tridacna*; filamentous algae within skeletons of living corals; encrusting filamentous, crustose coralline, and fleshy green algae affixed to smooth and rough surfaces; and algae associated with dead coral heads. They estimated, admittedly crudely, dry biomass of primary producers. In the coral–algal ridge zone, algae in corals and encrusting and free-living algae contributed about equally to the total estimate of 635 g m^{-2}. In the encrusting zone, encrusting algae and algae boring within the rock substrate accounted for most of the biomass. The estimates of Bailey-Brock, White, and Ward (1980) for comparable zones on an island platform are similar; the latter researchers reported order-of-magnitude lower biomass

TABLE 4

Distribution and Biomass of Algae Across the Windward Reef Platform at Enewetak Islet*

	Zone				
	Crest	4	3	2	1
Distance from shore (m)	85	60–71	40–60	20–40	0–20
Predominant algal species					
Porolithon spp.	70				
Jania sp.	10	60	60	25	5†
Dictyosphaeria cavernosa	5				
Padina japonica	5	10	} 5	} 5	
Caulerpa spp.		5			
Valonia spp.		25	5		
Boodlea composita		10			
Gelidiella sp.		10			
Polysiphonia sp.	5‡	5	5	5	
Cladophora hemisphaerica				2	
Codium edule				2	
Total percent cover	95	95	80–95	30–40	10–15
Mean dry wt (g m^{-2}) platform		850	625	65	65

*Data from Bailey-Brock, White, and Ward, 1980. Figures in body of table are percent cover.

†Includes *Acetabularia clavata*.

‡Includes *Ceramium* sp.

inshore (Table 4). The coralline *Jania capillacea* and the brown *Sphacelaria* sp. are predominant algae in the encrusting zone (Miller, 1983).

Benthic Fauna: Abundance and Distribution

Protozoa

Foraminifera containing symbiotic algae are the largest and most prominent benthic intertidal Protozoa at Enewetak. They are probably restricted to cracks and holes in the reef rock that afford both adequate light for photosynthesis and shelter from grazing fishes and invertebrates (Lipps and Delaca, 1980). These authors reported the presence of several genera at Enewetak but did not indicate which were intertidal. Hirshfield, Charmatz, and Helson (1968) noted that the family Miliolidae comprised 82% of the Foraminifera on the Parry (Medren) Island; seven rarer taxa were also present. Foraminifera containing zooxanthellae are often important contributors to both calcification and organic carbon fixation in coral reef associated communities (Smith, 1977). Benthic Foraminifera are sufficiently abundant occasionally to be important food items of some xanthid crabs (Havens, 1974) and fishes (Hiatt and Strasburg, 1960).

Porifera

Clionid sponges that excavate chambers in the hermatypic coral *Porites lutea* on interisland platforms are ecologically the most important Porifera of the Enewetak intertidal and shallow subtidal zones. The dominant species are *Aka* sp. cf. *A. diagonoxea* and *Cliona* sp. cf. *C. quadrata* (Highsmith, 1981). They initiate burrows as cylindrical excavations about 200 μm in diameter and 300 μm deep. The burrow is then extended 2 to 3 mm, after which it is expanded into a chamber 5 mm or more in diameter. Chambers of this size are found within 3 months of exposure of dead coral skeletal surface, especially on the undersides of *P. lutea* microatolls. Highsmith (1981) showed that sponges are the most common infaunal associate (in 86% of coral heads examined) and the most important bioeroders of corals at Enewetak. The overall effect of this bioerosion is not known. Smith (1973) suggested that the rate of $CaCO_3$ removal by sponges is probably something less than one-fourth the rate of calcification.

Cnidaria

The predominant cnidarian of low intertidal (+0.15 to 0.3 m; Havens, 1974) interisland platforms is the hermatypic coral *Porites lutea*. Here its typical growth form is the microatoll. As described by Highsmith (1980), "the tops of these massive corals are killed by prolonged exposure during seasonally low tides. The coral tissue around the periphery of the head survives and continues to grow radially outward resulting in the characteristic microatoll form." *Porites lutea* microatolls tend to become detached from their substrate because (1) their inability to maintain live tissue under shaded portions of the periphery results

in an overhang of tissue-covered, growing skeleton, and (2) they are weakened by the skeletal boring activity of clionid sponges and sea urchins. Detached, living pieces of *P. lutea* microatolls tend to move lagoonward across the interisland flat in the unidirectional water flow. They consolidate in a zone along the lagoon edge, where they contribute importantly to active reef growth (Highsmith, 1980). Odum and Odum (1955) noted the presence of less abundant corals; these are listed above in the description of the coral–algal ridge taken from their paper. They referred the anemones they noted to the genus *Actiniogeton*. Miller (1983) noted a common, undetermined high and mid-intertidal anemone.

The most abundant intertidal hydroid is the inconspicuous tropical and subtropical cosmopolitan species *Dynamena crisioides*. Its irregular branching stems extend 5 to 15 cm from a thick hydrorhiza, but it is often obscured by heavy encrustation of detritus and algae. It occurs intertidally in beachrock crevices at the north end of Enewetak Island and commonly on the outer portion of the island reef platform (Cooke, 1975).

Annelida

As on reef platforms elsewhere dominated by algal turfs (Kohn and Lloyd, 1973; Kohn and White, 1977), polychaete annelids are a numerically dominant component of the benthic invertebrate community at Enewetak. Blocks of reef limestone chiseled from the central portion of the windward Enewetak Island platform, including the overlying algal turf, support a mean density of about 90,000 polychaetes m^{-2} (range 82,000 to 100,000; 27 to 39 species; biomass 7.4 to 9.3 g m^{-2} dry weight). About 10% of the polychaetes (mean 8000; range 400 to 32,700 m^{-2}; 2 to 34 species) were associated with the algal turf alone, indicated by samples of turf scraped from the reef rock surface (Bailey-Brock, White, and Ward, 1980).

Species richness, population density, and biomass of polychaetes increased from shore toward seaward edge, with maxima at 56 to 66 m, closely paralleling the biomass of algal turf (Table 4, Fig. 3). Nearshore tidepools that hold more water than the surrounding platform support higher densities of polychaetes but not greater algal biomass. Near the coralline-dominated algal ridge (85 m from shore; Table 4), limestone blocks contained an estimated 60,000 polychaetes of 25 species m^{-2} (Bailey-Brock, White, and Ward, 1980).

Also typical of similar habitats elsewhere (Kohn and Lloyd, 1973; Kohn and White, 1977), the family Syllidae are both the most diverse (31 species) and the most abundant (up to 48,500 m^{-2}) polychaete family on the Enewetak windward platform (Bailey-Brock, White, and

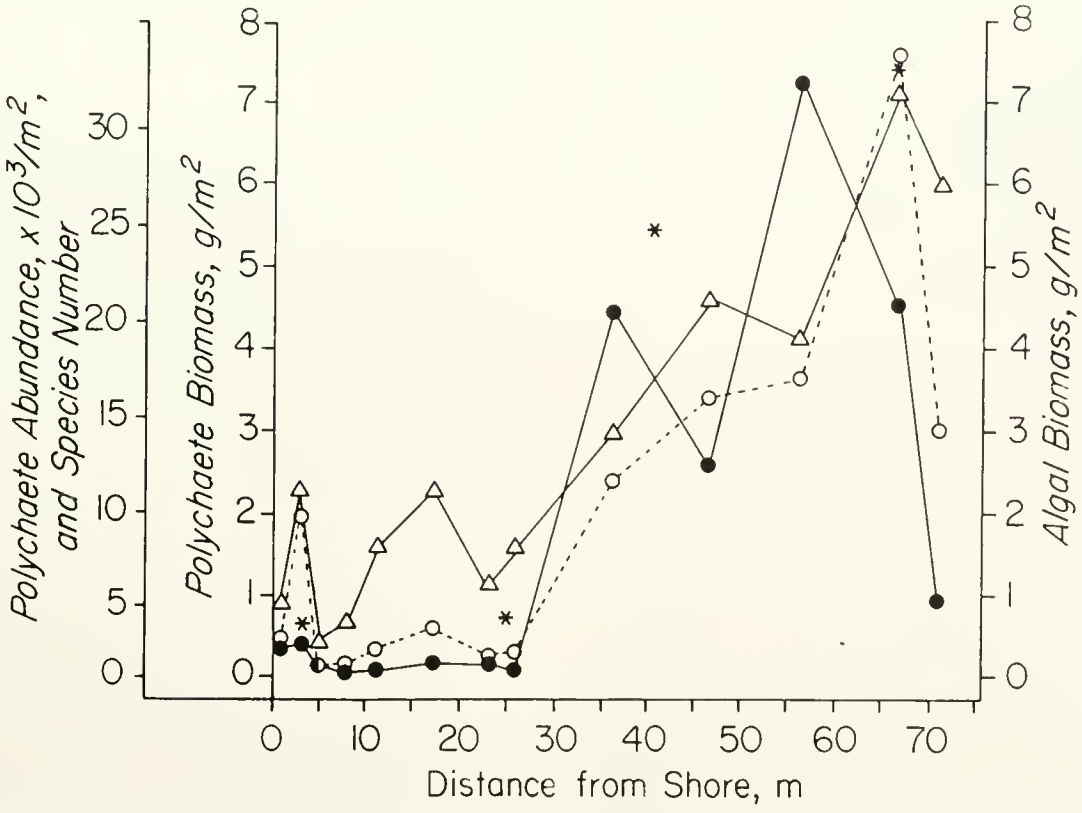

Fig. 3 Algal biomass and species richness, abundance, and biomass of polychaetes along a shoreward-to-seaward transect on the windward island platform at Enewetak Island. From Bailey-Brock, White, and Ward (1982).

Ward, 1980). However, most syllids are among the smallest polychaetes present. Their contribution to biomass is small in proportion to their numbers; however, their productivity is unknown and may well be very high. Tubicolous members of the families Spionidae, Sabellidae, Capitellidae, and *Dodecaceria* (family Cirratulidae), and the errant Syllidae predominated in the samples within 30 m of shore where algae are sparse. In the central portion of the platform with algal turf, the latter four taxa, Chaetopteridae, and the errant Amphinomidae are the most abundant polychaetes. The thick layers of smooth, encrusting coralline algae of the ridge support primarily Nereidae, Syllidae, *Vermiliopsis* (Serpulidae), Spionidae, and Eunicidae.

Polychaetes are also the most common invertebrates associated with *Porites lutea* heads on the interisland platform (Highsmith, 1981: App. II, Part C, Nos. C1, C3, C4, C5, C6, C9, 39, 41, 84, 87). Syllids dominated numerically (121 individuals), followed by eunicids (67, but with the greatest biomass), and cirratulids (60) in a sample totalling 264 polychaetes from nine heads. Highsmith (1981) considered most of the polychaetes to be nestlers, mainly in empty chambers that had been excavated by sponges in the coral skeleton.

Sipuncula

The only information on the distribution of intertidal sipunculans at Enewetak appears to be Highsmith's (1981: App. II, Part C) report of limestone-boring species in the skeletons of *Porites lutea* microatolls on the interisland platform. Seven corals examined contained 58 sipunculans of at least seven species. *Aspidosiphon muelleri* comprised 60% of the sample. Other identified species were *Cloeosiphon aspergillus*, *Lithacrosiphon gurjanovae*, and *Paraspidosiphon gigas*. Sipunculans probably occur densely in the reef rock substrate of the platform; as noted below they are the sole food of a common predatory gastropod, *Mitra litterata*.

Echinodermata

The sea cucumber *Holothuria atra* is the most conspicuous invertebrate of the interisland windward reef platforms. Bakus (1973) estimated 0.1 m^{-2} north of Enewetak Island. Maximal densities of from 3 m^{-2} (Webb, DuPaul, and D'Elia, 1977) to 5 to 35 m^{-2} (Bakus, 1973) occur in areas protected from high water velocities and surf. The highest densities occur in depressions and gutters that retain water at low tide (Ebert, 1978).

The sea urchins *Echinometra mathaei* and *Echinostrephus aciculatus* are commonly associated with *Porites lutea* microatolls and dead coral heads. They shelter adjacent to these and weaken them by eroding skeletal material, presumably by mechanical action of both teeth and spines. The densest populations of these echinoids also occur on slightly subtidal portions of the Enewetak windward reef platform. Here densities of *Echinometra mathaei* reach 6.5 m^{-2} and *Echinostrephus aciculatus*, 1.1 m^{-2}; the two species have similar environmental requirements and are significantly positively associated (Russo, 1980). Although probably second in importance to sponges as bioeroders, the roles of these urchins in removing $CaCO_3$ has been estimated more quantitatively. Russo (1980) calculated erosion rate by the two species together as 325 g m^{-2} yr^{-1} on the mid-portion of the reef platform and at 108 g m^{-2} yr^{-1} on the outer platform, where urchin densities are lower. This represents removal of about 2 to 8% of annual $CaCO_3$ deposition (Smith, 1973).

At the seaward edge of some windward platforms, especially on Japtan Island, *Heterocentrotus trigonarius* occurs commonly, wedged in cavities on the outer portion of the coral–algal ridge. It is the only sea urchin species in this surf-swept zone, and its massive body wall and thick, heavy spines adapt it to this harsh environment. In addition, *H. trigonarius* appears to have a physiological requirement for considerable water movement (Ebert, 1982).

Ebert (1982) also estimated growth and mortality rates of *Heterocentrotus trigonarius* and *Echinometra mathaei* at Enewetak. The former is a long-lived species (probability of annual survival is 0.97) that grows slowly and has a low instantaneous annual mortality rate per individual (0.006). *Echinometra mathaei* grows an order of magnitude more rapidly but has a shorter life span (probability of annual survival is 0.42) and a higher and quite variable mortality rate (1.26 in 1978; 0.48 in 1979).

Mollusca

Small prosobranch gastropods are particularly characteristic benthic invertebrates of windward reef platforms. Detritus-feeding vermetids, mainly *Dendropoma psarocephala*, occur at densities of 150 to 1100 m^{-2} (Miller, 1983). Detritus-feeding and herbivorous members of the family Cerithiidae attain densities of 800 m^{-2}; *Cerithium alveolus* is the most common species (Miller, personal communication). The cowry *Cypraea moneta* occurs centrally on the reef platform, typically in male-female pairs, at densities of 0.2 to 0.7 m^{-2} and is more abundant in tidal pools on the platform (2.0 to 6.7 m^{-2}) and subtidally in the quarry (Renaud, 1976). Carnivorous neogastropods, represented most abundantly by the families Conidae and Muricidae and secondarily by the Mitridae, Buccinidae, and Vasidae, have been more intensively studied. The first two families represent about 50% and 40%, respectively, of the predatory gastropods present (Kohn and Leviten, 1976; Kohn, 1980). Substrate topography is the most important factor controlling population density and species diversity of these gastropods. Depressions in the bench surface that collect coral rubble and flatter areas with thick algal turf that binds sand provide refuge from the harsh physical stresses of desiccation and rain at low tide and heavy wave action at high tide, and probably from predation (Ayal and Safriel, 1982).

Population densities of *Conus* species and of other predatory gastropods are significantly higher on portions of

bench with algal turf or natural or artificial depressions than on adjacent smoother, barer bench of the type shown in Fig. 1b. Species richness of *Conus* and of total predatory gastropods is also significantly lower in the last microhabitat type (Table 5; Kohn and Leviten, 1976; Leviten and Kohn, 1980). The most common species of *Conus* are *C. ebraeus*, *C. sponsalis*, *C. chaldaeus*, and *C. miliaris*. Rarer species are *C. frigidus*, *C. flavidus*, *C. catus*, *C. rattus*, and *C. retifer*; the last two did not occur in the quantitative samples summarized in Table 4. The predominant muricids are *Morula granulata*, *M. uva*, *Drupa morum*, and *D. ricina*; less common are *D. arachnoides*, *Maculotriton serriale*, and *Thais tuberosa*. *Drupa morum* and *D. ricina* are as abundant on smooth, bare bench as they are where refuges are present. Their depressed, limpet-like shells and disc-shaped feet permit more tenacious adhesion to the substrate than the longer, narrower feet of most other gastropods present. *Vasum turbinellum* (family Vasidae) is the most common other gastropod present, followed by the mitrids *Mitra litterata*, *Mitra cucumerina*, *Vexillum cancellarioides*, and *Imbricaria punctata* (Kohn and Leviten, 1976).

Co-occurring species of *Conus* do not use different types of microhabitat (listed in Table 1) differentially. All species observed are typically (96% of individuals) inactive in refuges during daytime low tides, when physical stresses are probably harshest. Activity increases abruptly to a high level in all species in late afternoon and early evening, unless water flow is too strong (50 cm s^{-1}), as the animals move over the smooth bench surface and feed during the night. They do not home to the same site used the previous day, and we detected no evidence for competition for protected sites. These results led to the conclusion that the *Conus* species on the windward island platform at Enewetak partition neither microhabitat nor temporal resources (Leviten and Kohn, 1980).

A few nudibranch gastropods occur in protected sites on windward platforms. *Chromodoris geometrica*, *Okadaia elegans*, and a few other members of the superfamily Doridacea occur under rocks intertidally, and the aeolidiacean *Herviella mietta* occurs in tide pools (Young, 1967). Characteristic of inner zones of the windward platform is the abundant pulmonate limpet *Siphonaria normalis*, which occurs at population densities of 400 m^{-2} on flat substrate

TABLE 5

Abundance and Diversity of Predatory Gastropods in Different Microhabitats on Windward Reef Platforms at Enewetak*

Microhabitat type and census areas	Area sampled, m^2	Conidae		Muricidae		All predatory gastropods	
		No. of species	Density No. m^{-2}	No. of species	Density No. m^{-2}	No. of species	Density No. m^{-2}
Smooth, bare portions without refuges (A_1, A_2, A_3)	106	3	0.7	4	1.1	9	1.8
Smooth portions with algal turf binding sand (B)	20	5	2.5	5	4.4	11	6.9
Smooth, bare portions with natural refuges (C_1, C_3, C_6, C_8)	118	5	3.3	6	0.9	16	4.6
Smooth, bare portions with artificial refuges (C_2)	57	5	4.1	6	2.9	14	7.5
Totals (sample sizes in parentheses)	301	8	(688)	7	(526)	21	(1297)

*Data from Kohn and Leviten, 1976.

The different *Conus* species are typically zoned across island platforms, with the peak abundances of *C. ebraeus* closest to shore, *C. chaldaeus* and *C. coronatus* intermediate, and *C. sponsalis* closest to the outer edge. However, distributions vary at different study sites and at different times at the same site (Leviten and Kohn, 1980). In all four of these species, shell length decreases significantly with distance from shore, but in *C. ebraeus* and possibly *C. sponsalis* it increases again near the outer limits of their distribution.

that dries at low tide and to 3500 m^{-2} in shallow tide pools. Its body size and population distribution are determined by the foraging behavior of its predator, the prosobranch gastropod *Thais armigera* (Menge, 1973).

Siphonaria normalis also occurs commonly on a smooth, sloping beachrock shore on the lagoon side of Enewetak Island at the +0.6- to +0.9-m level. It becomes active when just covered by a rising tide or just uncovered by a falling tide, moving from its home scar in an unpredictable direction to forage on microalgae (Cook and

Cook, 1981). After foraging, *S. normalis* returns to its home scar over its outbound route (Cook and Cook, 1978). Activity ceases for long periods of emersion during neap tide periods. Cook and Cook (1981) found no relation between distance moved and either body size or grazing interval in *S. normalis*.

In general, gastropods inhabiting the windward reef platforms are small in comparison with congeners occupying subtidal reef habitats. Few *Conus* exceed 25 mm in shell length in the former habitats (Kohn, 1971, 1980), and extensive field observations suggest the same to be true for other gastropod taxa.

Arthropoda

Xanthid crabs are the most prominent intertidal Crustacea at Enewetak. Havens (1974) studied their distribution and comparative ecology and presented detailed information on their habitats and habits. He listed the most abundant species by zones as follows. (Population densities are given in parentheses.)

Windward Buttress Zone and Coral-Algal Ridge. *Paraxanthias notatus* most common, then *Liocarpilodes integerrimus* and *Cycloxanthops cavatus*, associated with both dead coral and coralline algae; *Globopilumnus globosus* and *Dacryopilumnus emerita* in algal rock on the highest parts of the algal ridge; *Chlorodiella laevissima* on dead coral, and *Trapezia* and *Tetralia* spp. in living corals. Crabs other than xanthids in this zone include species of *Pachygrapsus*, *Percnon*, and *Plagusia* (Grapsidae) and *Thalamita* (Portunidae).

Inner Portion of Algal Ridge. *Eriphia scabricula* on coralline algal mounds; this species, *Dacryopilumnus rathbunae* (14 m^{-2}), *Liocarpilodes biunguis* and *L. pumilis* (5 m^{-2}) in the rims of rubble-filled former surge channels; *Lydia annulipes* (10 m^{-2}) on inner algal mounds.

Smooth Reef Platform. *Liocarpilodes biunguis* (33 to 104 m^{-2}; this is the most common intertidal xanthid in the Marshall Islands), *Xanthias lamarcki*, *Etisus bifrontalis*, and *Pilodius areolatus* in broad, shallow tidal pools such as the swale at our Sta. F7 described above (Leviten and Kohn, 1980: Fig. 1). The most diverse crab fauna of all intertidal environments Havens studied at Enewetak occurs here, including representatives of the families Atelecyclidae *(Kraussia)*, Portunidae *(Thalamita, Portunus)*, Grapsidae *(Pachygrapsus, Percnon)*, Ocypodidae *(Macrophthalmus)*, Majidae *(Micippa)*, and Parthenopidae. On the northern part of the Enewetak Island windward platform the algal turf is reduced to a film of blue-green algae, possibly because of grazing by herbivorous fishes at high tide as noted earlier. Here *Liocarpilodes biunguis* and *Leptodius davaoensis* (29 m^{-2}) are the most common xanthids, and *Leptodius sanguineus*, *Eriphia scabricula* (9 m^{-2}), and *E. sebana* also occur. At night, the last species is the most prominent large crustacean. The grapsid species mentioned above also occur here. The xanthid fauna of the innermost part of the platform is restricted to small *Liocarpilodes biunguis* and *Pachygrapsus minutus* that occur uncommonly in small holes.

Scalloped and Pitted Reef Rock. The dominant xanthid here is *Lydia annulipes* (10 m^{-2}), found in holes and crevices.

Beachrock. Ridges of exposed, intertidal beachrock occur adjacent to both seaward and lagoonward sides of islets (Kohn, 1981: Fig. 1) at Enewetak. The predominant xanthid crabs in seaward beachrock areas are *Pseudozius caystrus*, *Lydia annulipes*, and *Liocarpilodes biunguis*. Holes and cracks in intertidal beachrock on the lagoon side are an important habitat of *Eriphia scabricula* (15 m^{-2}). *Eriphia sebana* and *L. annulipes* (2 m^{-2}) also occur here.

Rubble-Covered Beaches. Loose coral rubble often covers sand and gravel of beaches at Enewetak; this is particularly apparent on the windward side after storms (Kohn, 1980: Fig. 1a). This habitat supports a characteristic crab fauna of the xanthids *Pseudozius caystrus*, *Leptodius davaoensis*, *L. gracilis*, and *L. sanguineus* (2 m^{-2}) and the grapsid *Pachygrapsus planifrons*. *Leptodius davaoensis* is more common than *L. gracilis* in the low intertidal (16 vs. 4 m^{-2}), but the latter tends to replace the former in the high intertidal (15 vs. 5 m^{-2}). *Pseudozius caystrus* attains a density of 21 m^{-2} even higher on the beach. Species of *Pseudograpsus* and *Cyclograpsus* occur higher, on sand under rocks at the supratidal fringe.

Porites Microatolls. The highest diversity of Xanthidae at Enewetak occurs on interisland reef platforms in association with the *Porites* microatolls discussed previously. Among the 35 species of xanthids are *Pilodius areolatus*, *P. pilumnoides*, *Xanthias lamarcki*, *Liomera bella*, *L. pallida*, *Chlorodiella cytherea*, *C. laevissima*, *Paramedaeus simplex*, *Medaeus elegans*, *Etisus bifrontalis*, *E. demani*, *Lachnopodus subacutus*, and *Carpilius convexus*, and the portunid *Thalamita picta*. Highsmith (1981: App. II, Part C) noted a somewhat different set of crabs in this habitat. He also reported acrothoracican barnacles in the coral heads.

Havens (1974) considered the five species listed in Table 6 as the characteristic low intertidal xanthids of Enewetak. As the Table indicates, they tend to partition microhabitat resources. Table 6 also lists the three characteristic high intertidal species; the vertical distributions of the two sets of species do not overlap in the localities studied. These species also occupy quite distinct microhabitats from each other. Because *Eriphia scabricula* and *Lydia annulipes* occur at the same localities and occupy similar microhabitats but at different heights, they are good indicators of tidal level.

A large crustacean not seen on windward reef platforms during the day but active there at night is the macruran *Panulirus penicillatus*. During the day, it remains in subtidal dens on the reef front. Its major peak of activity follows dusk, when it crosses the reef crest to forage; a minor peak occurs at dawn. At Enewetak Island, it was observed to use primarily depressions covered with a thin

TABLE 6

Vertical Zonation and Microhabitats of the Eight Dominant Intertidal Xanthid Crabs at Enewetak*

Species	Primary microhabitat
Low Intertidal Species (Approximately +0.3 to −0.9 m)	
Liocarpilodes biunguis	Reef flats, in small holes†
Eriphia scabricula	Reef flats without algal turf binding sand, in large holes†
Leptodius davaoensis	Reef flats with thick algal turf; under small rocks‡; in large holes
Leptodius sanguineus	Reef flats and rubble-covered beaches; under large rocks‡ and overhangs; overhangs in large holes
Dacryopilumnus rathbunae	Eroding algal rock, beachrock, reef blocks with thin algal film; in sipunculan burrows (small holes)
High Intertidal Species (Approximately +0.8 to +1.3 m)	
Pseudozius caystrus	Reef flats and rubble-covered beaches; under large rocks mainly on gravel; less common on sand under rocks;
Lydia annulipes	Eroding reef rock, beachrock; in large holes
Leptodius gracilis	Reef flats and rubble-covered beaches; on sand or gravelly sand under rocks of all sizes

*Data from Havens, 1974.

†Small holes have aperture size (height + width) <17 mm; large holes have aperture size >17 mm.

‡Small rocks are <23 cm long; large rocks are >23 cm long.

layer of algae; at Ananij it occurred most commonly on a reef with *Porites lutea*, *Acropora* spp., and mats of the brown alga *Turbinaria*; at Enjebi it occurred in larger expanses of coral, primarily *P. lutea* and some *Acropora* spp. (McCollum, 1981).

Of the six species of shallow water stomatopods at Enewetak, *Gonodactylus incipiens* is the most abundant, uses the widest range of habitats, and occurs most commonly in the intertidal zone. It is often seen in isolated shallow tidepools. Smaller individuals predominate in the higher, inshore portion of the windward platforms. The other species are mainly subtidal, but *Haptosquilla glyptocercus* occupies coral rubble and holes constructed by other invertebrates on the windward platform, and it is active in tide pools. *Gonodactylus platysoma* is associated with the bases of microatolls on the intertidal platform northeast of Enewetak Island, and *G. micronesica* and juveniles of *G. smithii* occur in rubble in the same region (Reaka and Manning, Volume II, Chapter 17, this publication).

Of the few smaller intertidal crustaceans known from Enewetak, the amphipod *Melita celericula* occurs on the undersides of rocks from mid-intertidal to subtidal. In a transect on the lagoon side of the north end of Enewetak Island it reached densities of 104 m^{-2} at tidal levels of 0.2 to 0.3 m (Croker, 1971). In this habitat, it was associated with other species of amphipods as well as with isopods and tanaids.

Hermit crabs, primarily *Clibanarius corallinus* (54% of total censused) and *Calcinus laevimanus* (38%), occur on the Enewetak windward platform at densities of 3 to 65 m^{-2} (Miller, personal communication).

Benthic Fauna: Trophic Roles and Interactions

Although the standing crop, number, and biomass of several intertidal benthic invertebrate taxa have been assessed at Enewetak, very few quantitative data exist on their rates of resource utilization or their population dynamics. This section is thus mainly limited to summarizing available information on the roles of the numerically or biomass-dominant taxa, and others that have been studied, in the trophic structure of their community.

Suspension and Deposit Feeders on Small Particles

Tube-dwelling polychaetes predominate numerically in this category, especially where depressions retain water at low tide near shore on island platforms. Here the family Spionidae, chiefly *Pseudopolydora antennata* and *Microspio microcera*, averages 4300 individuals m^{-2}. These animals are selective detritivores. With a pair of long, tentacle-like palps they catch food particles both in suspension and deposited on the substrate. The numerically dominant suspension feeder is an unidentified filter-feeding sabellid polychaete (5900 m^{-2}). Next in abundance is the deposit-feeding capitellid polychaete *Leiochrides* sp. In the encrusting zone, common polychaetes in this category are the chaetopterid *Phyllochaetopterus ramosus* and the cirratulid *Cirriformia semicincta* (Bailey-Brock, White, and Ward, 1980).

Even less conspicuous than the polychaetes but bionomically important are sponges of the genera *Cliona* and *Aka*, the most important boring organisms of coral skeletons at Enewetak (Highsmith, 1980, 1981); they also penetrate reef limestone. Tropical sponges effectively remove a high proportion of particles in the 1-μm range from the water they pump through their bodies, and unlike other suspension feeders they are able to subsist exclusively on bacteria and smaller particles (Reiswig, 1971).

The most conspicuous deposit-feeding invertebrate on interisland platforms is *Holothuria atra*. From analysis of its gut contents, fecal pellets, and the surrounding sediment, Webb, DuPaul, and D'Elia (1977) showed this sea cucumber to feed selectively on materials considerably richer in organic content than the adjacent sediment, and they calculated its feeding efficiency at 40%. A median-sized *H. atra* (60 g) passes about 80 g (dry weight) of sedi-

ment a day. Webb et al. (1977) estimated that they dissolve about 1% of the ingested $CaCO_3$, equal to 2.5 g m^{-2} d^{-1}, or to about 25% of the net calcification rate on the reef flat.

Planktivores

Odum and Odum (1955) estimated dry biomass of corals at about 100 g m^{-2} in the coral–algal zone and of corals and anemones in the encrusting zone at about 50 g. They classified them as herbivores because of their utilization of zooxanthellae, but the predominant intertidal coral, *Porites lutea* (Highsmith, 1980, 1981), probably also feeds on zooplankton at night.

Inshore, the hydroid *Dynamena crisioides* is presumably a planktivore.

Herbivores

Herbivory by invertebrates on the windward reef platforms has been most thoroughly studied in crabs of the family Xanthidae. Of the eight common species studied by Havens (1974), seven are primarily herbivorous. In these, 78% to 100% of all individuals examined contained algal food in their stomachs. Table 7 summarizes their feeding habits and food based on Havens' findings. Predominantly herbivorous nereid and eunicid polychaetes (author's observations) also occur in the outer zones, but they are much less abundant than particle-feeding polychaetes (Bailey-Brock, White, and Ward, 1980). Centrally on the reef platform, the cowry *Cypraea moneta* eats primarily *Jania capillacea*, to which it is preferentially attracted by distance chemoreception (Renaud, 1976). Inshore, small but numerous herbivores include the pulmonate limpet *Siphonaria normalis*, a grazer on microscopic algae (Menge, 1973; Cook and Cook, 1978, 1981), and cerithiid prosobranch gastropods.

Odum and Odum (1955) estimated herbivore biomass at about 23% and 8% of plant biomass on the coral–algal ridge and encrusting zones, respectively, of the interisland reef. They considered corals and the sea urchin

TABLE 7

Feeding Habits and Food of the Predominant Intertidal Xanthid Crabs of Enewetak*

Species	Feeding habits				Food; specific foods (see key below) in approximate order of importance
	When	Where	How	What	
			Low Intertidal Species		
Liocarpilodes biunguis	Night	In open	Scrapes thin (1 mm) algae from rock; pulls bunches of algal filaments away from rock	Herbivorous	Plants (1, 3, 4, 2, 5)
Eriphia scabricula	Day + night	In open	Pulls thick algal turf from rock;	Omnivorous	Plants (3, 4, 1, 2, 5) Animals (5, 6, 7, 2, 3)
Leptodius davaoensis	Mainly night	Tide pools	As in *Leptodius biunguis*	Herbivorous	Plants (3, 1, 2)
Xantho sanguineus	Mainly night	Tide pools	As in *Leptodius biunguis*	Herbivorous	Plants (2, 3, 4, 1, 5)
Dacryopilumnus rathbunae	Day + night	In open or feed from holes	Scrapes thin algae from rock around shelter holes	Mainly herbivorous	Plants (1, 4, 3, 2) Animals (8, 5)
			High Intertidal Species		
Pseudozius caystrus	Always under cover		No observations	Omnivorous	Plants (3, 1, 2, 5, 4)
Lydia annulipes	Mainly night	In open	Pulls hole-dwelling prey from shelters; pries *Siphonaria* from rock; eats thick algal turf	Carnivorous	Animals (3, 4, 6, 2, 7, 1) Plants (1, 3)
Leptodius gracilis	Mainly night	Tide pools	Scrapes thin algae from rock	Herbivorous	Plants (1, 3, 4)

*Data from Havens, 1974.

Key to plant foods: 1, blue-green algae; 2, *Jania*; 3, *Polysiphonia*; 4, *Laurencia* + similar forms; 5, *Ceratocentrum*.

Key to animal foods: 1, Foraminifera; 2, polychaetes; 3, sipunculans; 4, *Siphonaria*; 5, small Crustacea; 6, crabs; 7, insects; 8, mites.

Heterocentrotus trigonarius to be the most important herbivores.

On the undersides of rocks, the amphipod *Melita celericula* may be primarily herbivorous. In the laboratory it fed on the algae *Valonia* and *Acetabularia* as well as detritus, fecal pellets, and small conspecific individuals (Croker, 1971).

Carnivores on Encrusting Animals

Only the abundance of polychaetes in this category has been quantified (Bailey-Brock, White, and Ward, 1980), and their feeding biology has not been studied. The amphinomids *Eurythoe complanata* and *Pseudeurythoe oculifera* occur in the outer or encrusting zone of the Enewetak Island platform 40 to 70 m from shore; they are closely related to species known to feed primarily on corals. Many members of the numerically dominant Syllidae probably belong to this category; some are reputed to feed on sponges, but despite their dominance little is known of their biology.

Chromodoris geometrica and other doridid nudibranch gastropods probably also feed on sponges (Young, 1967). Other nudibranchs whose food is known include *Herviella mietta*, which eats the eggs of the prosobranch *Cerithium sejunctum*, and *Okadaia elegans*, which eats spirorbid polychaetes after drilling a hole through the calcareous tube with its radula (Young, 1967).

Predators

The most important predatory invertebrates at the primary carnivore level are probably gastropods of the families Conidae, Muricidae, Mitridae, Vasidae, and Buccinidae. The food subwebs they participate in were being studied by the author and Paul J. Leviten at the time of the latter's untimely death in 1980. It is hoped this study will be concluded in the future, but preliminary results can be mentioned here. The pattern of trophic relationships in the food subweb in which gastropods are the primary carnivores (Fig. 4) suggests that species of *Conus*, the most abundant genus, prey primarily on members of different families from the other vermivorous gastropods. Within *Conus*, preliminary results indicate a general pattern of specialization on different polychaete taxa by the co-occurring species. Most similar to *Conus* diets are those of *Drupa morum*, which eats mainly eunicids, and *D. arachnoides*, which eats only nereids (Bernstein, 1974). As noted above, these limpet-like muricids are better able to exploit the more exposed, seaward portions of the platform where nereid and eunicid polychaetes are inaccessible to *Conus*. *Drupa ricina* eats mainly vermetid gastropods (92% of the diet: Bernstein, 1974). Two vermivores of different families, *Engina mendicaria* (Buccinidae) and *Vasum turbinellus* (Vasidae) prey on polychaetes of two families not utilized by other predatory gastropods. Their diets are very similar to each other, but their sizes differ strikingly; shells of the former average 12 mm long (range 8 to 18 mm) and those of the latter, 23 mm (range 15 to 32 mm). Finally, *Mitra litterata* (family Mitridae) feeds exclusively on sipunculans.

One uncommon *Conus*, *C. retifer*, and several abundant muricids prey primarily on herbivorous gastropods. *Morula granulata* eats mainly cerithiids (author's unpublished observations), and the diet of *Thais armigera* consists almost entirely of *Siphonaria normalis* (Menge, 1973). In addition, some of the species listed in Table 7 occasionally prey on molluscs.

Several xanthid crabs are also important primary carnivores on windward, seaward platforms, beachrock outcrops, and lagoon-side rocky shores (Havens, 1974). The upper intertidal *Lydia annulipes* is primarily a predator: 84% of stomachs examined contained animal remains and 28% contained plant food. Sipunculans and *Siphonaria normalis* are the main prey organisms (Table 7), either or both occurring in two-thirds of the individuals examined. In contrast, these organisms were not commonly eaten by the omnivorous xanthids *Pseudozius caystrus* (4%) and *Eriphia scabricula* (18%) or the partly carnivorous *Dacryopilumnus rathbunae* (1%). The diets of xanthid species that co-occur in the same microhabitats differ strikingly. For example, where *L. annulipes* and *P. caystrus* use the same crevices for shelter, the former feeds mainly on sipunculans and the latter on large crustaceans and algae (Havens, 1974).

A recent study of the macruran *Panulirus penicillatus* (McCollum, 1981) has provided considerable information on its prey. The several types of microhabitats frequented by *P. penicillatus* during foraging have been noted. McCollum's results suggest that *P. penicillatus* is a nearly omnivorous predator (Table 8); its diet is very diverse and did not differ significantly among locations studied at Enewetak. *Panulirus penicillatus* crushes its prey and swallows all the parts, so prey organisms with shells or other hard structures can be enumerated from stomach contents. Numerically, molluscs, crustaceans, and miscellaneous items ranked about equally; polychaetes and echinoids predominated in the last category. Although biomass estimates were not possible, a measure of importance based on number, volume, and occurrence indicated molluscs to be about twice as important as crustaceans and about eight times as important as miscellaneous items (McCollum, 1981). The stomach of one female *P. penicillatus* contained remains of 56 individual cerithiid gastropods, 52 individuals of *Strombus* sp., three trochids, and one *Fragum fragum* (Bivalvia); the gastropods were enumerated by counts of opercula. Another female had eaten many *Fragum fragum*, one *Pinctada* sp., at least two mytilids, 57 *Strombus* sp., 21 muricids, probably mainly *Morula* spp., nine cerithiids, including *Cerithium alveolus*, one each of *Mitra cucumerina*, *Pusia cancellarioides*, *Conus* sp., and *Natica* sp., and unidentified gastropods. On reef areas with more polychaetes and hermit crabs, higher proportions of these were consumed. In general, individual stomachs contained a high diversity of prey items (McCollum, 1981).

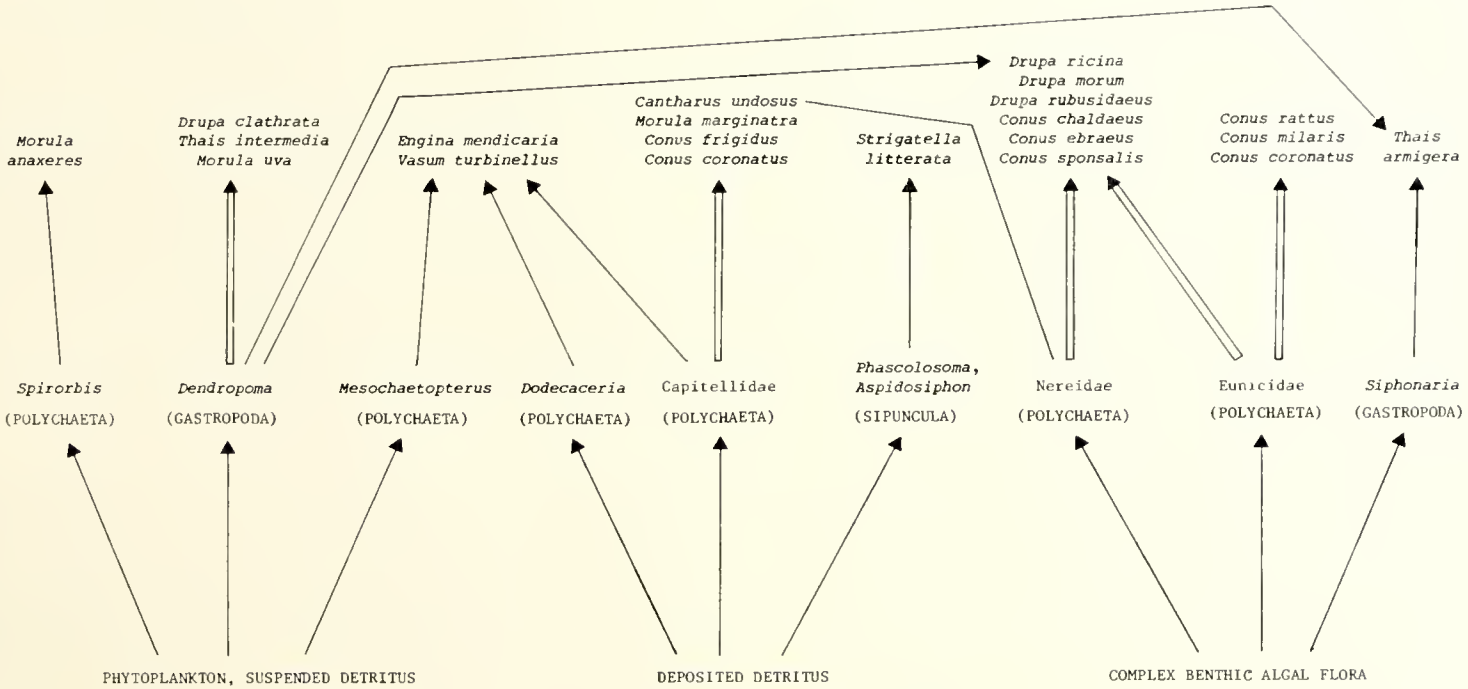

Fig. 4 Qualitative representation of trophic relations in the food subweb with gastropods as primary carnivores on the windward intertidal reef platform at Enewetak Island. Arrows indicate the direction of material and energy flow. Double arrows indicate predators in multiple listing above may differentially specialize on subordinate taxa of prey below. Based on unpublished data of A. J. Kohn, P. J. Leviten, and A. C. Miller and on Bernstein (1974).

TABLE 8

Major Prey Items of *Panulirus penicillatus* on Three Reef Platforms at Enewetak

	Number* of prey items
Mollusca	
Gastropoda	94
Bivalvia	30
Polyplacophora	33
	94
Crustacea	
Brachyura	84
Anomura	31
Hoplocarida	13
Other	9
	96
Miscellaneous	
Polychaeta	53
Echinoidea	26
Madreporaria	19
Ophiuroidea	16
Pisces	4
Algae	23

*Numbers in body of table are numbers of prey taxa at left recovered from examination of 78 *P. penicillatus* stomachs (McCollum, 1981).

UTILIZATION OF INTERTIDAL HABITATS BY FISHES

Windward platform surfaces dominated by a film or thin turf of the blue-green alga *Calothrix crustacea* are grazed intensively by fishes. Miller (1983) observed about 530 fishes per hour at high tide swimming through a 3 × 5 m quadrant on the northern part of the Enewetak Island platform. About 85% of these were herbivores, mainly parrot fishes and surgeonfishes. The predominant species are *Scarus frontalis, Acanthurus triostegus*, and *A. guttatus* (Hiatt and Strasburg, 1960; Bakus, 1967; Webb and Wiebe, 1975; Miller, 1983). "Their teeth marks in the reef rock provide evidence of the thoroughness with which they crop this alga" (Wiebe, Johannes, and Webb, 1975). "The most striking phenomenon about the reef flat is the innumerable toothmarks that range from the uppermost reaches of the dead coral substratum to the outer edge of the algal ridge, and beyond" (Bakus, 1967).

As the incoming tide covers the platform, large schools of *Acanthurus triostegus* "gradually browse their way to the uppermost reaches of the reef flat" (Bakus, 1967). Behind them are large schools (about 300 to 400 fishes) of the larger *A. guttatus*, then numerous schools of *Scarus* spp., which remain in slightly deeper water, venturing close to shore only between mid-tide and high-tide level (Bakus, 1967). Analyses of *Scarus frontalis* and *S. gibbus* indicated that both species graze only on dead coral and filamentous algae on reef rock. They consume considerable $CaCO_3$, which is acidified in the gut and reduced in particle size. These fishes commence feeding at first light (about 0730 at Enewetak). Less than 4 hours later, all individuals (mean standard length 31 cm) had full large intestines. Feeding continues until dusk (about 1900), at which time most individuals contained food in the anterior digestive tracts. Six hours later, all portions of all digestive tracts examined were empty (Smith and Paulson, 1974). These authors thus calculated transit time of food through the alimentary tract of 6 hours.

Juvenile *Acanthurus triostegus* also browse only on algae; stomachs of adults contain mostly algae but with a few small coral fragments. *Acanthurus guttatus* graze "significant quantities of coral fragments along with benthic algae" (Bakus, 1967). Analysis of tooth scars by Bakus (1967) showed that small tooth marks of *A. guttatus* and juvenile scarids predominate in the inner 18 m; scars of acanthurids and scarids intermingle over most of the platform; and the algal ridge, surge channels, and pools of the outer edge have mainly scarid scars.

From his estimate of net primary productivity of blue-green algae noted above and by estimating the biomass of herbivorous fishes utilizing the platform, Bakus (1967) concluded the *Calothix crustacea* and *Schizothrix calcicola* synthesize organic matter at a rate adequate to support the feeding activities of the fishes. These are, however, time-limited by periods of high tide and probably cannot meet their entire energy requirements by feeding only on the windward platform.

Other herbivorous fishes on seaward platforms at high tide are the browsing rabbitfish *Siganus argentatus* and, near the surf-swept outer edge, the surgeonfishes *Acanthurus achilles* and *Zebrasoma veliferum* (Hiatt and Strasburg, 1960).

That the limitation of algal cover on the more barren regions of the platforms is due to grazing has been demonstrated by Miller (1983) who reported 100% coverage of the platform surface by macroscopic algae after 3 months under 5-mm mesh cages that excluded grazing fishes and crabs but not smaller herbivorous invertebrates. Invertebrate abundance also increased in the exclosures.

Algal cover grades strikingly from the thin film of *Calothrix* and *Schizothrix* at the north end of the Enewetak Island seaward platform to a turf of erect, macroscopic *Jania, Sphacelaria,* and other forms about 300 m south. There fish grazing intensity is only about 30% of that observed farther north. The southern portion is probably less accessible to herbivores because of its greater distance from suitably sheltered subtidal sites required by the fishes at low tide, such as the quarry on the north part of the platform and the lagoon (Bakus, 1967; Kohn and Leviten, 1976; Miller, 1983).

Omnivorous fishes on the seaward platforms include the common blenny *Istiblennius coronatus*, which eats sur-

face sediment, filamentous algae and the foraminiferan, *Calcarina;* the triggerfish *Rhinecanthus aculeatus* (main foods: algae, gastropods, isopods, crabs, shrimp, polychaetes, fishes); and the damselfish *Abudefduf sordidus* (main foods: algae, crabs, fishes, polychaetes, *Calcarina*) (Hiatt and Strasburg, 1960).

Use of intertidal windward platforms by carnivorous fishes at high tide is poorly documented. The black-tip reef shark *Carcharhinus melanopterus* is frequently seen there but constituted less than 0.5% of all fishes observed by Miller (1983). This species is piscivorous (Hiatt and Strasburg, 1960).

UTILIZATION OF INTERTIDAL HABITATS BY BIRDS

Shorebirds of several species fly to the windward intertidal platform to feed at low tide. Johnson (1979) reported that whimbrels *(Numenius phaeopus),* bristle-thighed curlews *(N. tahitiensis)* and wandering tattlers *(Heteroscelus incanus)* use intertidal habitats more intensively than the other common Enewetak shorebirds, golden plovers *(Pluvialis dominica fulva)* and ruddy turnstones *(Arenaria interpres).* However, I have observed several occasions when golden plovers were the only common birds on the windward platform at Enewetak Island.

Bristle-thighed curlews are known to eat the prosobranch gastropod *Nerita* sp. by picking up the snail in the tip of the beak, raising the head, swinging the bill laterally and then across the back, and finally hurling the snail downward against the rocks. This procedure may be repeated several times until the shell is broken; the bird then extracts the snail's body (Carpenter, Jackson, and Fall, 1968).

BEACH AND SUPRALITTORAL FRINGE HABITAT

The most conspicuous invertebrates of the uppermost intertidal and supratidal beaches are ghost crabs of the genus *Ocypode.* Two species occur, *O. cordimana* extending from just below high-tide line to well up in the zone of fringing beach vegetation, and *O. ceratophthalma,* ranging downward from about high-tide line. The latter species is more common, but both tend to occur on the same beaches. Both live in burrows during the day and are active nocturnally. Little is known of their ecology, but at night *O. cordimana* usually sits near its burrow entrance, retreating within at the slightest disturbance. Only *O. ceratophthalma* wanders over the beach at night. In the account from which the preceding information was taken, Horch (1975) compared acoustic and other aspects of the behavior of these species.

In the wave-washed zone of sand beaches in Enewetak Lagoon, the predatory anomuran crustacean *Hippa pacifica* is prominent nocturnally. Mysid crustaceans, caught with hairs on the long first pereiopods, are its main food at Enewetak (Wenner, 1977).

Among the few meiofaunal taxa reported from Enewetak are tardigrades of the genera *Hypsibius* and *Macrobiotus,* found in supralittoral fringe beach sand (Mehlen, 1972).

EFFECTS OF ENVIRONMENTAL DISTURBANCES ON INTERTIDAL BIOTA

In recent years several cases of mass mortality of tropical intertidal organisms from severe storms or other episodic catastrophes have been documented. These are cited by Leviten and Kohn (1980), who described the effects on gastropod populations of an unusually severe rainstorm that coincided with a low tide that left the inner 40 m of the windward platform at Enewetak emersed for several hours. On Sept. 3, 1972, 4.3 cm of rain fell during a 6-hour period. A strong smell of rotting organisms persisted for more than a week after the storm during low tide periods, attesting to the death of many types of organisms. Of 155 individuals of six species of *Conus* censused in the area on Sept. 6, we found that 70% (83/119) of *C. ebraeus* and 92% (33/36) of the five other species were killed. Thus the species whose distribution normally extends farthest inshore, *C. ebraeus,* had the highest survivorship. The nearly total mortality of all other species in the affected area suggests that unpredictable catastrophes such as rainstorms may prevent them from occupying inshore areas of bench. Mortality of *C. ebraeus* was also size-selective: all individuals <15 mm long were killed, while 38% of those >15 mm survived (not 15%, as erroneously reported in Leviten and Kohn, 1980). Thus the observed size-frequency distributions of *Conus* species noted above may also be determined by variations in physical stress across the platform (Leviten and Kohn, 1980).

It was also possible to assess the effects on intertidal gastropods of another severe environmental disturbance, Typhoon Alice, which struck Enewetak Jan. 5, 1979. On the central portion of the Enewetak Island platform, where thick algal turf had provided protected sites for gastropods, the turf was much thinner and population density of *Conus* species was much lower after the typhoon. However, on the portion of the platform where cracks, crevices, and rubble-filled depressions on otherwise smooth, bare bench were the main refuges, there was no significant reduction of *Conus* abundance or species richness. Predatory gastropods other than *Conus* species, predominantly (94%) Muricidae, were not significantly reduced in number of individuals or species in the latter area and were reduced less than *Conus* species in areas with algal turf, probably due to the greater tenacity of muricids as described above (Kohn, 1980). Predatory gastropods on the windward reef platform are thus behaviorally adapted to use refuges that shelter them adequately from the most severe storm conditions likely to be encountered there. In six of 10 comparisons involving *C. ebraeus, C. chaldaeus,* and *C. sponsalis* at several sites,

size-frequency distributions were shifted significantly toward larger shell lengths after the typhoon, suggesting size-selective mortality with smaller individuals more likely to die, as in the case of rainstorm-induced mortality.

CONCLUSION

The intertidal zone, populated almost exclusively by plants and animals of marine origin, exposes these organisms to the harshest physical conditions and widest amplitudes of fluctuating physical variables of any oceanic environment. On an atoll, heating and desiccation from tropical insolation, inundation by heavy rain, and storm waves exacerbate even these stringent conditions. Nevertheless, complex and highly productive biotic communities characterize the intertidal component of atoll ecosystems. At Enewetak, studies over the past 25 years have documented the major outlines of community organization and have revealed some important, unexpected characteristics. This chapter has summarized the knowledge they have provided of the identity of the major organisms present, their population densities, distribution patterns, temporal variations, habitat requirements, and trophic roles and interactions. However, a satisfactory synthetic model of intertidal community structure and processes will require more intensive future studies of trophic dynamics and of both biological and physical factors affecting the composition and relationships of the biota.

Note Added in Proof

Recent analysis of the microhabitats and diets of a large sample of three species of *Drupa* collected by Paul Leviten on the seaward, windward platform in 1972–74 amplifies the study of Bernstein (1974) reported in the text (Thomas and Kohn, 1985).

Drupa morum, the largest species (mean shell length 25 mm) and the one occupying the most exposed, seaward microhabitats, preys primarily (65% of diet) on nereid polychaetes (*Ceratonereis mirabilis* and *Perineresis singaporiensis*) and secondarily (23%) on eunicid polychaetes (*Eunice afra* and *Lysidice collaris*). *Drupa ricinus* (mean shell length 22 mm) is more widely distributed across the platform. In its more exposed microhabitats it preys primarily on vermetid gastropods *(Dendropoma gregaria)* and perhaps other species of the genus. In inner, more protected areas it preys more frequently on nereids, mainly *C. mirabilis*. Overall its diet comprised 44% vermetids, 42% nereids, 5% other polychaetes, and 9% crustaceans. *Drupa arachnoides* (mean shell length 20 mm), the most inshore species, preys almost exclusively (92%) on *C. mirabilis*. Overall, predator size and prey size were positively correlated.

DEDICATION

Much of the author's research at Enewetak was carried out in collaboration with Paul J. Leviten (Fig. 5), whose untimely death from cancer in 1980 at age 36 deprived tropical marine ecology of a gifted and productive scientist. Leviten was educated at the Universities of Miami (B.S. and M.S.) and Washington (Ph.D.). He was a Queen's Fellow for 2 years in Australia, and he served on the faculties of the University of California at Irvine and Santa Barbara.

Fig. 5 The late Dr. Paul J. Leviten at work in the Mid-Pacific Research Laboratory, Enewetak.

Leviten was the sole author or co-author of four major papers, all of which reported research performed at Enewetak. His research blended mastery of theory, quantitative field ecology, and devotion to knowledge of the Mollusca in harmonious proportions, and his accomplishments contributed significantly to all of these. This chapter is therefore dedicated to his memory.

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Chapter 9

Reef Processes: Energy and Materials Flux

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INTRODUCTION

A number of significant studies of reef community processes have been conducted at Enewetak. These studies have made major contributions to an understanding of that particular system. Their significance also lies in the development of methodology and of a general approach to understanding whole ecosystems. Such studies have strongly influenced the context in which many ecologists think about reef systems and have probably had a broader influence on ecology generally.

One of the earliest and most important studies, conducted during the first year of Enewetak Marine Biology Laboratory (EMBL) operations, was that of Odum and Odum (1955). This was a remarkable attempt to look at the reef ecosystem as a whole and to relate structure to function. It has been widely cited not only by reef researchers but also by other ecologists and has had an impact on ecology generally. It generated great interest both for its approach and for its specific findings and conclusions. The Odums did an impressive amount of work during their 6 weeks at the field site and then used this as the basis for far-reaching extrapolations. Additionally, they stimulated a great deal of interest in reefs as ecosystems and prompted many other researchers to undertake further studies, apparently if only to prove the Odums wrong in some cases. Their seminal study thus occupies a central position in a chapter on ecosystem processes of Enewetak.

A more recent study utilizing the same approach was conducted by the SYMBIOS team in 1971 (Johannes et al., 1972). The team, consisting of some 25 scientists with a variety of diverse but related interests, spent 2 months studying transects near the earlier Odum transect. This much larger scale effort confirmed and extended many of the original findings of the Odums in a repeat demonstration of the utility of the upstream–downstream sampling methodology and particular processes and phenomena.

In addition to community metabolism, other important studies to be discussed in this chapter have focused on calcification processes at the ecosystem and organismal level, on nitrogen and phosphorus cycling, on the role of detritus (coral mucus and algal fragments), on coral nutrition, and on ecological relationships of reef fishes. Noteworthy research gaps include the lack of attention directed to ecological relationships involving humans and the apparent dearth of information on the impact of atomic testing, even though EMBL and the operations it evolved into have been supported by the Atomic Energy Commission and its successor organizations.

Several other papers resulting from work at Enewetak are often cited and have had a major influence on the thinking of reef scientists. These include papers by Goreau (1959), Hiatt and Strasburg (1960), and Muscatine (1967). Other papers of general interest are those by Knutson et al. (1972), Smith (1973), and Hobson and Chess (1978).

It is noteworthy that the work supported at EMBL and its successors includes few general descriptive studies. There are perhaps two reasons for this. First, much of the descriptive information that is available was accumulated incidentally during the course of other types of studies. Second, and perhaps more important, much information was previously available as a result of extensive surveys (some of them quantitative) during Operation Crossroads. Hence, much of the descriptive background for more functional studies was already available when EMBL began operations. Nevertheless, additional descriptive information, with an emphasis on quantitative observations, would probably be helpful.

The large number of geological, physical, and geochemical studies carried out at Enewetak makes this one of the most thoroughly studied reef systems in the world. It is ironic that much of this information is still apparently scattered in various sources, especially unpublished ones, and perhaps available only in the files of different funding agencies. A careful synthesis of such potentially available information might lead to a more comprehensive overview of the Enewetak ecosystem than is otherwise possible—an overview based on more than an "expedition" mentality. It is thus unfortunate that the ecosystem with the greatest

potential for an integrative understanding of reef processes, and the greatest realized development of such an understanding to date, has not seen this potential fully developed.

Most of the studies of Enewetak processes have focused on reef flats rather than deep faces or lagoons. Indeed, "reef" is synonymous with "reef flat" for many researchers. There is some justification for this position since this is the portion of the reef system that receives the greatest inputs of solar energy required for primary productivity and has been shown to be the most actively calcifying portion of the system (Smith and Harrison, 1977). It also appears to be the major site of nitrogen fixation (Wiebe, 1976). Finally, at least as a first approximation, the reef flat appears to be the source of the major nutrient and energy inputs to the lagoon, the most extensive subsystem of the atoll. Indeed, the impression shared by many reef ecologists is that the comparatively small, intensely productive reef flats provide the major inputs driving the whole system.

DESCRIPTIVE STUDIES OF REEF STRUCTURE

The general picture that many people have of biological zonation on reefs, especially Pacific atoll reef flats, is strongly influenced by the description provided by Odum and Odum (1955). They described a series of zones extending roughly parallel to the breaking surf on the windward reef margin and perpendicular to the direction of water flow across the reef flat. They also provided estimates of the standing crops of dominant reef organisms. This built upon extensive earlier descriptions by Tracey et al. (1948) and Emery et al. (1954). The former paper provided a general system of classification for various reef types and made the distinction between island reefs and interisland reefs on atolls. The Odums' description applies generally to at least some fringing reef flats (e.g., Marsh, 1974) as well as to atolls. Their work still stands as a useful general description of reef flats.

The Odums distinguished six zones on their reef, proceeding from seaward to lagoon. The *windward buttress zone* constitutes the seaward face of the reef outside breaking surf; it was inaccessible to the Odums but they estimated that there is about 50% coral coverage on the submarine buttresses in this zone. The *coral–algal ridge zone* is dominated by calcareous red algae and fleshy algal mats, with scattered encrusting forms of *Acropora*, *Pocillopora*, and *Millepora* corals. Behind this the *encrusting zone* likewise has sheets of yellow encrusting *Acropora* and *Millepora* and low, rounded heads of *Porites* and several species of favid corals. Filamentous algae of all four major benthic algal divisions form heavy encrusting mats here. Coral cover is far less than 50%. Next is the *zone of smaller heads* with massive heads of *Porites lobata* and favid corals; encrusting *Acropora* is not present but scattered colonies of branching corals of the genus can be found. The *zone of larger heads* is slightly deeper and has massive heads up to a meter high and 2 m across, with sand channels between the heads. The blue octocoral *Heliopora* is common here, with a distinct narrow zone of the stinging coral *Millepora* at the back edge of the zone of larger heads. Parrotfishes and surgeonfishes commonly browse and school here. Algal cover is much lower in the zones of smaller and larger heads than in the two zones immediately upstream. The *zone of sand and shingle* has very low occurrences of either algae or corals and few of the fishes found in the upstream zones; however, there are schools of sardine-like fishes that feed on "pseudoplankton" (algal fragments) drifting downstream in the current. To the Odums, the reef structure suggested a transition from water-filtering as a source of nutrients in upstream zones to subsurface decomposition as a source of plant requirements in back reef zones.

Odum and Odum (1955) attempted to get biomass estimates of the different trophic levels for different reef zones. This was an ambitious undertaking that has not been repeated, presumably because of the large amount of work involved and the uncertainties of assigning particular organisms to specific trophic levels. An attempt to repeat their estimates in the light of more recent information on the basic biology of the organisms involved is obviously called for in a variety of reef ecosystems.

The Odums estimated the dry weights of primary producers by chlorophyll extractions (based on Harvey pigment units) calibrated by establishing a ratio of chlorophyll to dry weight for the free-living macroalga *Codium*. This was done for free-living algae of various growth forms, for zooxanthellae contained in the living tissue of coral polyps, and for filamentous green algae ("boring" algae) within the skeletons of corals and other calcareous material. The mean estimate for producers averaged over all reef zones was 703 g dry biomass m^{-2}, with little evident difference in the producer component of live corals from different reef zones. The white sand area of the back-reef zone was found to be the only major reef zone with a definitely lower biomass of producer organisms. From data on colonization of glass sides left on the reef, the Odums calculated the growth of encrusting algae on the front reef to be twice that on the back reef, consistent with the observed predominance of encrusting forms in the former zone and boring forms in the latter zone.

Animal biomass at the primary consumer level (second trophic level) was reported by the Odums to consist primarily of fish, coral polyps, molluscs, echinoderms, annelids, and crustaceans, depending upon the particular reef zone. The measured biomass averaged 132 g dry weight m^{-2} for all reef zones combined. The third trophic level was found to consist primarily of predatory fish, molluscs, crabs, annelids, and starfish, averaging 11 g dry wt m^{-2}. The ratio of herbivores to producers was calculated to be 18.9% and of carnivores to herbivores, 8.3%. This resulted in a pyramid of biomass with a broad base and a small peak, a result stressed by Odum and Odum as being consistent with ecological theory.

COMMUNITY STUDIES

Oxygen Metabolism and Primary Productivity

The seminal nature of the Odum and Odum (1955) study has been noted. Theirs was not the first upstream–downstream study of reef metabolism, being preceded by that of Sargent and Austin (1949, 1954). It succeeded, however, in generating widespread interest and is probably responsible for the frequently made statements that reef systems are oases of high productivity surrounded by nutrient-poor deserts, that they are among the most highly productive systems on earth, and that they are highly efficient transformers of solar energy into biological energy. The Odums' work was also responsible for promoting the knowledge that it is the benthic community rather than the phytoplankton in the overlying water which is responsible for this high productivity. These are all key elements in our present understanding of reef ecosystems.

More precise and thorough measurements of community metabolism were carried out by the Project SYMBIOS team (Johannes et al., 1972; Smith, 1973; Smith and Marsh, 1973), but the basic conclusions reinforced those of the Odums regarding the high productivity of the windward reef flat. The team further provided at least a partial answer to the commonly asked question of how reefs could be areas of such high productivity surrounded by nutrient-poor and unproductive oceanic waters. It concluded that high rates of nitrogen fixation and extremely efficient internal recycling of phosphorus were major factors. This conclusion was later disputed by Atkinson (1981), whose work is discussed in the section on community phosphorus cycling.

Smith and Marsh (1973) made simultaneous measurements of oxygen and carbon dioxide changes in water as it flowed across the windward reef flat. The two independent estimates gave strongly correlated results for daytime productivity values but a weaker correlation for nighttime respiration values. These results allowed them to make the first estimate of the metabolic ratio (i.e., the molar change in CO_2 per molar change in oxygen) for a reef community. They found this ratio to be -1, uncorrected for diffusion, and suggested that corrections for diffusion without some indication of the metabolic ratio did not increase precision of productivity measurements.

Smith and Marsh compared two reef-flat transects, one similar to that described by Odum and Odum and containing coral zones as well as algal zones, and one transect of similar length but crossing no coral zones. The algal transect had a much higher gross P, net P, and gross P:R ratio (based on a 24-h period) but had similar rates of respiration, perhaps reaching an upper limit imposed by diffusion rates of oxygen to the large benthic infaunal community. Their coralgal transect had an overall gross P:R ratio near 1 and was apparently just self-sufficient with respect to energy demands. Assuming, however, that the algal portion of the coralgal transect was metabolically similar to the algal transect, Smith and Marsh calculated that the coral portion of the former transect was heterotrophic. Thus, there appeared to be an upstream autotrophic portion and a downstream heterotrophic portion for that transect. They postulated that the large schools of herbivorous fishes migrating between reef zones could be significant in transferring energy and materials downstream. Perhaps more attention should be directed to the question of whether this distinction of an upstream autotrophic and a downstream heterotrophic zone is a general feature of reef-flat ecosystems, as originally suggested by Odum and Odum. Much more comprehensive studies of community metabolism, especially of reef flats, have been made at other study sites by Kinsey (1977, 1979).

Wells (1974) and Wells et al. (1973) described a method for making in-situ measurements of benthic metabolism in reef communities and presented some preliminary results. Their basic technique was to place a transparent plastic dome over a suitable portion of the substratum and to monitor oxygen changes in the enclosed water mass in the light and in the dark. Preliminary measurements were made at Enewetak on the SYMBIOS transect and at sites in the Virgin Islands. At Enewetak, enclosed water masses were reported to show a rather constant oxygen concentration of 125% saturation while gas bubbles were being produced in the light; the oxygen content of the evolved gas was 28 to 32%. The oxygen evolution of algae-covered pavement reached a maximum of 5.5×10^{-3} ml cm^{-2} h^{-1} with a maximum P:R ratio (24-h basis) of 1.6. Coral rubble was observed to produce at about half the rates of the algae-covered pavement. These preliminary attempts to measure metabolic activity of the algal pavement thus focused on a neglected, but probably major, component of the reef-flat ecosystem. Marsh likewise has made a few unpublished measurements of small sections of such pavement removed from the reef and placed in respirometers. His preliminary values for gross P ranged up to 0.087 mg O_2 cm^{-2} h^{-1} and suggested that this might be one of the most metabolically active segments of the reef-flat ecosystem; this should be followed up.

Calcium Carbonate Production and Reef Growth

While there were several earlier attempts to estimate the growth rates of individual reef components, especially corals (e.g., Mayor, 1924), one of the first attempts to assess calcium carbonate deposition directly for the reef community as a whole was made by Smith (1973). Along with concurrent work by Kinsey in Australia (1972), this research pioneered the technique of utilizing changes in pH and alkalinity as water flowed across a reef flat not only to assess organic productivity but also to evaluate the dynamics of calcium carbonate deposition and dissolution at an ecosystem level. Smith found that both a coralgal transect and a transect dominated by an algal turf calcified at an

average rate of 4000 g $CaCO_3$ m^{-2} yr^{-1}. There were no apparent differences between day and night in these studies. Smith further calculated that, although there was little particulate $CaCO_3$ removal from the reef flat over the duration of his studies, there has been virtually no net $CaCO_3$ accumulation on the windward reef flats of Enewetak over the last several thousand years. He thought that lagoonward accumulation is the probable sink for calcareous material produced on the reef flat but that sediment transport occurs almost exclusively during periods of intense wave action.

The observation that daytime and nighttime calcification rates for the whole community are similar ran counter to much previous thinking, which was strongly influenced by the measurements of individual organisms enclosed in small containers. For instance, Goreau (1961) reported that calcification rates in individual corals, as measured by uptake of ^{45}Ca, were strongly light-dependent. However, Smith pointed out, as had others before him (e.g., Chave et al., 1972), that there are large uncertainties inherent in using the standing crop and turnover of individual organisms to estimate $CaCO_3$ production of the community as a whole. Furthermore, it is likely that corals, which are most often used in the individual-organism approach, account for a minor component of total calcium carbonate production on a reef. Smith also pointed out that the technique of measuring alkalinity depletion as a way to estimate $CaCO_3$ deposition could be applied in incubation chambers with individual organisms. Smith (1974) stated in a later paper that community precipitation of $CaCO_3$, ranging from -0.02 to 0.2 moles $CaCO_3$ m^{-2} d^{-1}, is an order of magitude lower than the calculated CO_2 flux resulting from organic carbon metabolism (± 0.2 to 6 moles d^{-1}), although the former process is not reversible on a day–night cycle and the latter process is. Flux due to diffusion across the air–sea interface or to mixing of water masses is likewise an order of magnitude lower than that resulting from organic carbon metabolism.

Smith and Kinsey (1976) combined the data and ideas generated by the Enewetak research with those from reef research elsewhere to make some generalizations about calcium carbonate production and sea level change. They suggested that shallow, seaward portions of most modern reefs produce approximately 4 kg $CaCO_3$ m^{-2} yr^{-1}, and that "protected" areas produce about 0.8 kg. They argued that the difference in these rates is probably due largely to differences in water motion. The more rapid rate is equivalent to a maximum vertical accretion of 3 to 5 mm per year and places an upper limit on the potential of modern coral reef communities to create a significant vertical structure during a rising sea level. They suggested that the major taxa accounting for most $CaCO_3$ deposition rates are corals, coralline red algae, and calcareous green algae; the potential reef accretion, however, does not appear to be affected by coral versus algal dominance. They found little evidence for latitudinal gradients.

Smith and Harrison (1977), using dome enclosures placed over the benthic community and following pH and alkalinity changes in the enclosed water mass, assessed calcium carbonate production of the *mare incognitum* on the upper seaward reef slope, a habitat barely considered in any previous study of any type. They made measurements on "vasiform" *Acropora* heads and on algal pavement but not on sand and rubble substrata. Smith and Harrison reported that calcium carbonate production by the corals is substantially lower on the seaward slope than at the control site (a subtidal quarry on the reef flat of Enewetak Island) and that it may decrease with depth. Production by algal pavement was also reported to be lower on the slope than at the control site but showed no apparent reduction with depth. However, calcium carbonate production by algal pavement in the quarry was dramatically slower than that by algal pavement on the reef crest. The coral calcification rate (on a square-meter basis) was always greater than that for algal pavement by a factor of 3 to 9. As in other reef habitats, it was recognized that topographic inequalities of the *mare incognitum* increase the effective surface area by up to 50%. Smith and Harrison concluded that the most actively calcifying portion of an atoll is near sea level, even though standing crops of calcifying organisms on the reef flat may be lower than on the reef slope. This is consistent with assumptions inherent in earlier studies that the major metabolic activity is on the reef flat rather than in other subsystems of the atoll. Their presumed optimum environment for reef development is a broad shoal area only a few meters deep with exposure to oceanic swells.

Nitrogen Flux

It was Odum and Odum (1955) again who first considered nitrogen flux on reefs and made a few measurements of changes in nitrate and ammonium as waters flowed across the windward reef flat. Gilmartin (1960) likewise made a few measurements in lagoon waters by "standard oceanographic techniques," but the first extensive measurements of any nitrogen compounds were made during Project SYMBIOS (Johannes et al., 1972; Webb et al., 1975). The researchers observed changes in various nitrogen species as water flowed across the usual coralgal or exclusively algal transect and found that both transects showed a significant net export of combined nitrogen, implying a large input of nitrogen into the system from a source other than combined nitrogen in incoming waters. Following up on this observation, they found that there were high rates of gaseous nitrogen fixation in the reef ecosystem, the first time that this process had been reported for any such system. The transect dominated by algae showed a net uptake of nitrate–nitrogen, and there was a net export of that species from the coralgal transect. Other nitrogen species (ammonium, dissolved organic nitrogen [DON], and particulate organic nitrogen [PON]) likewise increased significantly in waters flowing across this transect. The DON concentrations (2300 to 3000 nmol) were about an order of magnitude higher than the PON values. On this transect, there was a net removal of NO_3^-

on the algal portion and a net release on the coral portion. There were no significant day–night differences, but there was greater export of NH_4^+, DON, and total N during noon-to-midnight periods than during midnight-to-noon periods. The C:N ratio decreased progressively from offshore (15:1) to the lagoon (6.6:1). There was a major input of organic nitrogen to downstream portions of the coralgal transect, mainly in the form of algal fragments broken off from the surf zone. The blue-green alga *Calothrix crustacea* seemed to be a major nitrogen fixer; heterotrophic bacteria were apparently not important in this process since fixation was strongly light-dependent. The increase in POC as water crossed the reef flat was proportionately less than that of total nitrogen. Webb et al. calculated that 1000 kg N ha^{-1} yr^{-1} was exported from the reef flat, a high value that falls at the upper end of the range of nitrogen fixation values for managed agricultural plots. As we have already seen, this process of nitrogen fixation was invoked by Johannes et al. as an important part of the explanation of how reef ecosystems have high productivities in the midst of nutrient-poor oceanic waters. Nitrogen metabolism, like other metabolic processes, was clearly found not to be dominated by corals.

Webb and Wiebe (1975) made additional observations on the nitrification processes on a reef; they reported on in-situ and in-vivo incubations with and without an ammonium oxidase inhibitor and concluded that an autotrophic pathway involving two separate organisms was operating in the oxidation of ammonium to nitrate. The bacterium *Nitrobacter agilis* was found to be at least one organism responsible for the terminal oxidation of NO_2^- to NO_3^-.

A later paper, by Wiebe et al. (1975), also considered aspects of nitrogen fixation in a coral reef community. It suggested that, since algal flats fix nitrogen at rates comparable to those in managed agriculture, and this fixation contributes to high productivity of adjacent reefs and lagoons, algal flats should receive increased conservation priority. They further observed that *Calothrix crustacea*, the dominant nitrogen fixer, grows in two forms. One of these forms is a thin, yellow-brown, often almost unispecific film covering large portions of the intertidal reef flat. Most of this algal film remains moist at low tide; at high tide herbivorous fish (especially acanthurids and scarids) graze it extensively. Another growth form of *C. crustacea* occurs along the upper intertidal bench zone as a black, felt-like mat up to 5 mm thick; this mostly dries out at low tide and is not heavily grazed by herbivorous fish at high tide because the water is too shallow. The nitrogen fixation rates of moist samples of the upper intertidal form averaged only 60% of those of the reef flat (34 versus 55×10^{-9} moles h^{-1} cm^{-2}). However, per unit of horizontal map area, the actual surface area of coral and reef rubble is much greater than that on the algal flat and may, therefore, lead to comparable rates of nitrogen fixation for the two habitats, normalized to square meters of map area. Wiebe et al. further stated that the nitrogen fixed by *Calothrix* may enter the reef trophic web directly by grazing, through broken-off fragments, or through release into solution.

Wiebe (1976) summarized the above studies and further pointed out that salinities ranging from 2 to 45 ppt had no detectable effect on the rate of nitrogen fixation. Furthermore, the rate was temperature-dependent and approximately doubled between 27°C and 36°C, was 0 at 24°C, and increased for 2 hours then ceased at 39°C. The greatest upstream–downstream increase in concentration of nitrogen species was for DON, followed by NH_3 and NO_3^- in about equal concentrations. Not detected in the flow studies was NO_2^-.

Phosphorus Cycling

There are fewer studies of phosphorus cycling in the reef ecosystem as a whole. Odum and Odum (1955) made a few measurements of reactive phosphorus in waters flowing over the interisland reef, in waters entering the wide passage not far from their reef transect (presumed to be representative of oceanic waters outside the atoll) and in the lagoon. They reported levels of 0.26 to 0.64 μg atoms l^{-1} and concluded that there was a tight cycling of this element internally in the reef-flat community. Gilmartin (1960) likewise made a few measurements in lagoon waters and found generally low levels of the same order of magnitude as those reported by the Odums. Measurements by Pomeroy and Kuenzler (1967) were made incidentally to work with individual populations; their work is discussed later.

The first extensive measurements of changes in waters flowing across the reef flats were made by Pilson and Betzer (Johannes et al., 1972; Pilson and Betzer, 1973). They reported that the concentrations of reactive and organic phosphorus did not show detectable change in waters flowing across a coralgal transect but that there was a slight decrease in reactive P and a slight increase in organic P across a strictly algal transect. In particular, they found that concentrations did not vary in proportion to photosynthesis and respiration rates of the whole community, despite the fact that their ability to detect changes was at least two orders of magnitude more sensitive than would have been required to detect such changes if the Redfield (atomic) oxygen:phosphorus ratio of 138:1 was applicable in this system. Pilson and Betzer also found no diurnal variations in concentrations as waters flowed across the reef. This remarkable constancy suggested to them that the plants were taking up phosphorus at a nearly constant rate, regardless of the magnitude of photosynthetic activity. Their mean concentrations of P in flowing waters were 326 nmoles total P, 172 nmol reactive P, and 154 nmol organic P.

The conclusions of Pilson and Betzer were later challenged by Atkinson (1981), who worked primarily in Kaneohe Bay, Hawaii, but also made some observations at Enewetak. He found that exchange rates between reef benthos and the water column did not fit the Redfield ratio and concluded that changes in phosphate concentration of

waters flowing over the reef flat could be used as an indicator of community metabolism. He further argued that "recycling of phosphorus for a whole reef flat is not tight, and that the system can depend primarily on exchange with the water column for its nutrients."

Role of Regenerative Spaces

One aspect of ecosystem-level processes that has probably not received sufficient attention is the role of the extensive internal spaces of the reef in nutrient regeneration. DiSalvo (1969, 1971), in work conducted partly at Enewetak and partly in Kaneohe Bay, Hawaii, recognized the potential importance of these spaces and attempted to assess some of their quantitative aspects. He obtained bacterial counts of 10^4 to 10^5 bacteria per g dry wt and found that some isolated bacteria were capable of digesting chitin in vitro, suggesting there might be bacterial degradation of the organic matrix of coral skeletons (as opposed to the $CaCO_3$ making up the bulk of the skeletal mass). DiSalvo also obtained estimates of the oxygen demands of internal sediments amounting to 0.06 to 0.50 mg O_2 g sediment^{-1} h^{-1}; these rates were considerably lowered by antibiotics. The O_2 consumption of sediments in suspension was 10% of the total consumption by two intact heads. Water samples collected from within the regenerative spaces in situ generally showed oxygen debts as compared with ambient reef water. DiSalvo reported that the oxygen debts of inshore (stressed) reefs in Kaneohe Bay were greater than those of offshore reefs. It is curious that the role of internal spaces, which are quite extensive in reef systems, has not been the subject of more studies. Their potential significance seems great, but the preliminary work of DiSalvo has not received much follow-up.

STUDIES OF INDIVIDUAL POPULATIONS

Studies of energy and materials flux in individual reef populations have focused on the corals. There is a relative paucity of information about other populations. Furthermore, there has been no attempt (other than that of Odum and Odum) to investigate the role of individual populations and to integrate these roles to arrive at an estimate of whole-community function. There is thus a wide gap between ecosystem- or community-level studies on the one hand and individual-population studies on the other hand. However, several studies have certainly resulted in the implication, if not direct evidence, that the corals are a relatively unimportant component in total energy and materials flux; although they are visually impressive and are generally taken as characterizing the very essence of the reef, their role may be misinterpreted.

Algal Productivity and Growth

Marsh (1970) made one of the earliest attempts to assess the primary productivity of an individual algal population and evaluate its role in total reef productivity. He worked with encrusting forms of calcareous red algae, samples of which were removed from the reef and placed in respirometers in the laboratory. He measured an average gross photosynthesis of 0.048 mg O_2 m^{-2} h^{-1} under conditions of light saturation; the light-saturation intensity was reported to be 1000 ft-candles (less than 10% of full sunlight), with no photoinhibition at higher light intensities. Rates of photosynthesis and respiration in flowing water showed no correlation with different water velocities but were greater than rates in still water. Daily patterns of photosynthesis calculated for populations living on the submarine face of atolls suggested that light is probably not a limiting factor for that process during most daylight hours. Marsh calculated productivity for various calcareous algal zones and concluded that these zones do not contribute significantly to overall community productivity. Island reefs on atolls, where such zones account for a larger percentage of the total reef area, were estimated to be less productive than interisland reefs on the same atolls. Marsh stated that the productivity of calcareous algae is of the same order of magnitude as values reported in the literature for other benthic producers but is near the lower end of the range. His estimates, however, were based on the actual surface area of individual samples rather than the flat map area (for which 1 m^2 is occupied by more than 1 m^2 of irregular photosynthesizing surface). Marsh's values were thus underestimates as compared with those based on flat map area.

A study by Hillis-Colinvaux (1977) focused primarily on a field survey of natural distributions of various species of *Halimeda*. However, the author combined this with information from previous laboratory studies of photosynthesis and respiration of *Halimeda* from the Caribbean (Hillis-Colinvaux, 1974) to calculate productivity for some Enewetak populations. In localized reef and lagoonal areas where the coverage of these species approached 100%, Hillis-Colinvaux calculated that their productivity could be as high as 2.3 g C m^{-2} d^{-1} and could contribute a significant amount of energy to the total reef system. Hillis-Colinvaux further concluded that *Halimeda* populations contribute a significant proportion of the loose sediments in the atoll system, with seven species being the main contributors.

Bakus (1967) used a different approach in evaluating the primary productivity of "dense but thin" algal mats growing on the hard substratum of intertidal reef flats. He scraped off all the algae in small quadrats and weighed, combusted, and reweighed the harvested material to get an estimate of the initial organic standing crop. After placing exclosures over the scraped quadrats to keep out grazing fishes, he then repeated the scraping after 15 to 17 days to get an estimate of the productivity by the harvest method. The dominant species of the scraped algae were the blue-greens *Calothrix crustacea* and *Schizothrix calcicola*. Bakus' estimates of net daily production measured by this technique ranged between 0.6 and 2.15 g C m^{-2}.

One major conclusion of the Odums regarding the importance of an individual population received widespread

attention but can now be rejected. They found filamentous boring algae in almost all calcareous substrata they examined and concluded that this was a major contributor to total primary productivity of the system as a whole. This has been fairly conclusively disproved by the work of Kanwisher and Wainwright (1967), Franzisket (1968), and Halldal (1968). They presented evidence that very little light penetrates through the outer layers of coral tissue to the skeletal boring algae, which in turn saturate at low light levels and have low total photosynthetic output. It is thus unlikely that these boring algae play a significant role in either the nutrition of individual corals or the total productivity of the system.

All these individual population studies are preliminary, but they are the only attempts so far to make a statement about the contributions of particular populations to total productivity of the Enewetak system. Thus there continues to be a gap between whole-ecosystem studies and individual-population studies.

Coral Nutrition, Metabolism, and Growth

Several studies conducted at Enewetak have been concerned with one of the longest-running debates about any aspect of reef biology: how corals obtain their nutrition and the role of symbiotic zooxanthellae in meeting their energy requirements. Studies in this area started with the work of Yonge et al. on the Great Barrier Reef Expedition of 1929, and the ensuing debate of whether corals are "autotrophic" (i.e., obtaining all their energy requirements from their symbiotic algae) or "heterotrophic" (i.e., dependent on the capture of zooplankton for at least part of their energy requirements) continues to this day.

A significant contribution was made by Muscatine (1967), who demonstrated that zooxanthellae isolated from reef corals and giant clams incorporated radioactively labeled CO_2 during photosynthesis. In the presence of some component of host tissue, up to 40% of the labeled algal photosynthate was liberated from the algal cells, primarily as glycerol. Muscatine was unable to evaluate the rates at which this occurred in situ but suggested that excretion of glycerol by the algae and its control and utilization by the host may represent a mechanism whereby the zooxanthellae contribute to the productivity of reefs. The work of Muscatine has subsequently been widely cited and has been influential in shaping the way that researchers think about coral nutrition and its role in reef function, although quantitative determinations of transfer rates are needed.

Roffman (1968) worked with several species of intact corals (with their enclosed zooxanthellae) removed from the reef and placed in respirometers exposed to ambient sunlight, to reduced light levels resulting from various layers of screening, and to complete darkness. He calculated P:R ratios and concluded that some species have at least the capability of obtaining all their nutritional requirements from their symbiotic algae. This is representative of similar conclusions drawn from a variety of studies conducted at Enewetak and elsewhere; in fact, the research itself is representative of a commonly used approach in dealing with the question of coral nutrition.

Wethey and Porter (1976a, b) likewise used a respirometer approach in obtaining evidence for sun and shade differences in corals, as reflected in variable rates of net photosynthesis of individual colonies exposed to differences in the radiant-energy flux. Working with the foliaceous species *Pavona praetorta*, Wethey and Porter found that colonies from a depth of 25 m had a lower P_{max} (maximum rate of net photosynthesis) and a lower K_m (light level at which the intact coral–algal association photosynthesized at half its maximum rate) than colonies from 10 m. In this case, net P was expressed as mg O_2 mg chlorophyll a^{-1} h^{-1}; however, they did not report the amount of chlorophyll in the colonies from the two depths. Wethey and Porter estimated that the ratios of gross P:R for shallow and deep corals were 1.79 and 1.81, respectively, for sunny days and 1.44 and 1.50, respectively, for overcast days. A shallow-growing individual placed at 25 m was calculated to have a ratio of 1.08 on overcast days. Hence, shallow and deep colonies were considered to fare equally well under parallel weather conditions.

Wethey and Porter also estimated the percentage of gross photosynthesis needed to sustain the coral–algal association for 24 hours and calculated this to be 31% and 30% for shallow and deep corals, respectively, on sunny days and 45% and 42%, respectively, on overcast days. A shallow colony, if placed at 25 m, was calculated to require 68% of its gross photosynthesis on overcast days. According to Wethey and Porter, the acclimation of deep corals compensates completely for low available light. They stated that the species studied is morphologically specialized for autotrophy and is capable of a purely autotrophic existence down to 25 m, even under overcast conditions. They suggested that this species has acclimated to the worst conditions that it is frequently exposed to rather than to the worst conditions ever encountered on an infrequent basis. Their work appears to have important implications for coral nutrition and is beginning to be followed up.

There has been much interest in the physiology of skeletal formation in corals since the late fifties; important work in this field was done at Enewetak. Goreau (1959), in a paper which has been widely cited and which contains a widely reproduced schematic figure of the chemical pathways in calcification, employed the then-new technique of measuring ^{45}Ca uptake to examine the calcification process and factors influencing it. He reported that the rate of uptake of radioactive calcium was significantly lowered for corals incubated in the dark versus those incubated in the light. Furthermore, the calcification rate of corals held in darkness for long enough periods to cause expulsion of their zooxanthellae was considerably reduced but was apparently independent of light intensity. The existence of growth gradients for different parts of coral colonies was shown in a number of species. Calcium uptake was greatly reduced by a specific carbon anhydrase inhibitor; but there was still some uptake with complete inhibition, even in the

dark. Goreau concluded that the effect of light on coral growth is at least partly mediated through the zooxanthellae. A few experiments were also done with the calcareous red alga *Porolithon*. Goreau's pioneering study greatly influenced the thinking and research of later researchers.

Clausen and Roth (1975) looked at the effect of temperature and temperature adaptation on calcification rates in the coral *Pocillopora damicornis*. They reported that temperature has a marked effect on the rate of ^{45}Ca uptake but that the effect varies depending upon the temperature history of the coral (interpreted as meaning that temperature adaptation occurs). The temperature optimum shifted from 27°C to 31°C, depending upon the temperature at which the corals had been previously held. Clausen and Roth also noted the great variability in rates of ^{45}Ca uptake even when all experimental material and conditions were as constant as could be achieved.

Chalker (1976) studied the mechanism of calcium transport during skeletogenesis in the corals *Acropora cervicornis* and *A. formosa*. He found that light-enhanced calcification results from the active transport of calcium ions and shows saturation enzyme kinetics. On the other hand, dark calcification, as simulated by the addition of the photosynthetic inhibitor DCMU, results from enzyme-mediated isotopic exchange. Strontium was found to be a competitive inhibitor of both light-enhanced and dark calcification. Chalker concluded that his data refuted the diffusional model for calcium movement in hermatypic corals. He also reported that light-enhanced calcification creates a significant energy demand which may possibly be satisfied by the oxidation of low-molecular-weight compounds translocated from the symbiotic algae to animal tissue. In reference to the earlier work of Muscatine and subsequent researchers, Chalker suggested that other organic compounds besides glucose, glycerol, and alanine should be examined for such possible translocation.

Knutson et al. (1972) and Buddemeier et al. (1974), working at a different level of biological organization, reported cyclic variations in the radial density of coral skeletons, as revealed by X-radiography of thinly sliced samples. The presence of bands of radioactivity deposited in the coral structure by atomic testing at known dates allowed calibration of these growth bands, which were thus found to be annual. This "retrospective analysis" of coral growth opened up a new area of research which was then followed up by Buddemeier et al. The calibration procedure took advantage of the unusual situation created by previous atomic testing at Enewetak and could not have been accomplished at most other sites.

Knutson and Buddemeier (1973) followed up on the initial work by examining the distributions of radionuclides in reef corals. They reported that historic variations in the specific activity of surface oceanic ^{90}Sr and ^{14}C could be reconstructed from band-dated colonies. Studies of the ^{90}Sr content of Enewetak corals suggested that the lagoon community was acting as a long-term source of that radioisotope. Knutson and Buddemeier further reported that they could detect no significant changes in coral growth rates, patterns, or skeletal structures related to previous nuclear weapons tests.

Highsmith (1979) studied the relationship between coral growth rates and the environmental control of density banding in the massive species *Favia pallida*, *Goniastrea retiformis*, and *Porites lutea*. Of these species, *Goniastrea* has the densest skeleton but an intermediate growth rate; *Porites* grows more rapidly. All three species grow indeterminately and at a declining growth rate with increasing depth. *Favia* was found to have a linear growth rate of 5.7 mm yr^{-1} and a mass growth rate of 0.82 g cm^{-2} yr^{-1}; *Goniastrea* had rates of 6.8 mm yr^{-1} and 1.16 g cm^{-2} yr^{-1}, respectively; and *Porites*, rates of 7.6 mm yr^{-1} and 1.07 cm^{-2} yr^{-1}, respectively.

Highsmith found that the high-density portion of annual-band couplets is produced during late summer and fall when water temperature is highest and light is possibly reduced; low-density portions of the annual couplets are formed during seasonally lower temperatures and possibly higher light availability. In deeper water, the high-density portions of the skeletons account for a greater proportion of linear and mass growth than in shallower water; the high-density portions of the skeletons also account for a greater proportion in those corals with slower growth rates. This led to the prediction that linear growth will be highest where conditions are most favorable for deposition of low-density skeletal material. Highsmith further proposed that matrix production in the skeleton is more closely linked to activities of the zooxanthellae than is extracellular calcification and that the former tends to decline sharply at temperatures above or below the optimum of 27°C or with decreasing light. On the other hand, extracellular calcification is positively correlated with temperature, at least up to 31°C to 32°C.

Nitrogen Flux in Individual Populations

Interest in the nitrogen flux of individual populations has been slower to develop than interest in oxygen metabolism and calcification and has followed the previously discussed studies of nitrogen flux in reef communities as a whole. Aside from nitrogen-fixing algae and bacteria, interest has focused primarily on corals (e.g., D'Elia and Webb, 1977; Muscatine and D'Elia, 1978), with the large reef-flat populations of holothurians being the only other major population to be studied (Webb et al., 1977).

D'Elia and Webb (1977) studied dissolved nitrogen flux in corals and focused primarily on rates of nitrate uptake. Working with intact coral colonies in incubation chambers, they found uptake to be light-dependent. Uptake was localized in the coral tissue or its algal symbionts and did not occur in the bare skeletons left when living coral tissue with its contained zooxanthellae was removed. Uptake was found to fit the active-transport model of enzyme kinetics, with a half-saturation constant of 249 ± 247 nM and a maximum uptake rate of 5.69 ± 1.11 ng-atoms mg N^{-1} min^{-1} (29.9 ± 7.1 ng-atoms N mg chl a^{-1} min^{-1}). There appeared to be a threshold ambient nitrate concen-

tration (57 ± 47 nM) below which uptake did not occur. A limited number of organic nitrogen determinations indicated that a slight efflux of such compounds occurred. A model of nitrogen flux in *Pocillopora* species was produced in which, at typical ambient levels, ammonium uptake appeared to be about twice as great as nitrate uptake. D'Elia and Webb concluded that, while dissolved nitrogen taken by corals might be nutritionally important, it was not likely that the organisms could sustain high growth rates on this nitrogen source alone; hence, some ingestion of particulate nitrogen was probably necessary.

In a later paper, Muscatine and D'Elia (1978) studied ammonium flux in intact coral colonies held in incubation chambers. Of several species tested, only those containing zooxanthellae were found to take up and retain NH_4^+. Uptake and retention were enhanced by light, and the authors concluded that uptake during a normal daylight period is sufficient to sustain NH_4^+ retention during the night. The pattern of uptake kinetics for several species indicated that a two-process mechanism might be involved. When a diffusion correction was made, uptake kinetics could be characterized by the Michaelis-Menton equation. Corals without symbiotic algae were found to release NH_4^+ during incubation experiments.

Webb et al. (1977) assessed the biomass and nutrient flux in populations of the sea cucumber *Holothuria atra* which are abundant on the windward reef flats of Enewetak. They estimated average densities of three animals m^{-2}, with a median weight of 60 g, in the zone of small heads on a coralgal transect. Size distribution of individuals was found to be negatively correlated with water current velocity.

Ammonium release by the population was equivalent to 9% of total release by the reef community and was weight-specific in *H. atra, H. difficilis,* and *Actinopyga mauritiana* (i.e., the size-specific release rate was constant for different-sized organisms). Urea was also released by animals in incubation chambers. For *H. difficilis,* the total release consisted of 57% ammonium, 17% urea, and 26% unidentified nitrogen compounds in a 2-g animal. For all three species, the ratio of N:P release was 42:1 for 60-g animals and 25:1 for 1-g animals.

Webb et al. (1977) also analyzed reef-flat sediments and the gut contents and fecal pellets of *H. atra* for total and organic carbon. Of the total carbon in the sediments, 3% was estimated to be organic; 10% of the carbon in fecal pellets was estimated to be organic. The authors stated that this finding could be accounted for by the dissolution of $CaCO_3$ in the animals' guts, by selective feeding, or by both of these processes. The sediments were estimated to consist of 0.4% organic C and 12% inorganic C by dry weight; fecal pellets were 1.3% organic C and 11.6% inorganic C. The dissolution of $CaCO_3$ by holothurian populations was estimated to be approximately 2.5 g m^{-2} d^{-1}, equivalent to about 25% of the net calcification rate for the reef flat as a whole. Webb et al. concluded that *H. atra* is a selective feeder and that it ingests and egests materials considerably richer in organic carbon than the general sediment; assimilation efficiency was estimated to be approximately 40%.

Phosphorus Flux in Individual Populations

Studies of phosphorus flux in individual populations started before those of nitrogen flux and have been more numerous and concerned with a larger variety of organisms. The first was reported by Pomeroy and Kuenzler (1967), who examined phosphorus content and elimination rates for dominant reef animals of several taxa; these two measurements were then integrated to estimate the flux of P through the organisms, expressed as turnover times. Herbivorous fishes appeared to receive just enough P for growth and reproduction, as reflected in somewhat lower excretion rates and longer turnover times than would be predicted for organisms of their size by standard relationships. In the important herbivorous fish *Acanthurus* (turnover time, 410 days), the ingestion of small quantities of animal food, even if taken only incidentally to grazing on algal filaments, might be an important phosphorus source. Carnivorous animals and deposit feeders were calculated to receive excess P in their diets, with turnover times (12 to 4000 days for a large size range) not significantly different than they would be in ecosystems with a more abundant supply of that element. Of five coral species, four showed very long turnover times (10^2 to 10^3 days) and little P loss to the environment. The giant clam *Tridacna crocea* showed a typical turnover time (about 900 days) for a mollusc of its size, and most of its P loss was that incorporated into living zooxanthellae which were subsequently lost. In general, the phosphorus economy of animals containing algal symbionts seemed to be quite varied. Zooplankton had turnover times approximating 1 day.

Additional studies of the exchange of phosphorus between organisms and reef waters were conducted by Pomeroy et al. (1974). Although algal mats dominated by the blue-green *Schizothrix* showed an active uptake of radioactively labeled PO_4^{-3} in the light, they also showed a continuous loss. Pomeroy et al. thought that the loss was at high enough rates that, if a bell jar were placed over the pavement community for a short time in the dark, changes in dissolved phosphorus could be detected chemically in the enclosed water mass. They also considered it possible that as much as 50% of the photosynthetic products of the pavement community might be released as soluble organics containing no P. Algal mats dominated by the articulated coralline red *Jania* showed no net uptake or loss of phosphorus when incubated. Algal-encrusted pebbles showed an insignificant suggestion of uptake and no evidence of loss. The corals *Acropora* and *Heliopora* showed no net uptake or loss after equilibration, while *Millepora* showed continuous uptake. Compartmental analysis of the former two species suggested that there was a pool of phosphorus in the coral tissue in equilibrium with PO_4^{-3} in the ambient water and isolated from the P demand of the zooxanthellae. Pomeroy et al. cited Muscatine's earlier (1967) work as evidence that much of the photosynthate released from the

zooxanthellae contains no P; hence, the coral–algal association should require new P only for growth and replacement of zooxanthellae. Corals may thus recycle phosphorus (and nitrogen) so effectively that their requirements are met by the solid food they ingest, with no uptake from ambient water being necessary; this is possible only for a slow-growing community.

With respect to transfers between trophic levels, it was not clear to Pomeroy and co-workers which consumers benefit from the coral production, although mucus may be one of the major coral products (a recurrent theme which will be discussed further in the next section). Phosphorus in the algal filaments cropped by fish is probably recycled largely to PO_4^{-3} by excretion. At least 75% of such P may be recycled in 1 day in this kind of system. The authors found significant recycling of P in all reef communities examined. They concluded that the principal reef communities at Enewetak are not limited by P and have evolved either internal (biochemical) or external (food chain) recycling loops to satisfy apparent P demands. These conclusions were thus consistent with the ways that ecologists have thought of reefs since publication of the Odum and Odum paper.

Arsenate uptake and reduction by the coral *Pocillopora verrucosa* are somewhat related to phosphorus cycling and were examined by Pilson (1974). In incubation experiments, *P. verrucosa* was found to remove arsenate from solution and convert some of it to arsenite, which reappeared in the ambient seawater. This suggests that organisms other than bacteria may be responsible for maintaining some of the arsenic in seawater in a reduced form. Reduction of arsenate may be a mechanism to allow the loss from the living coral cells of arsenate incidentally transported in along with phosphate.

D'Elia (1977) further examined the uptake and release of dissolved phosphorus by corals in incubation experiments. He found that the net uptake of reactive phosphorus from seawater by corals containing zooxanthellae was not sufficient to offset simultaneous losses of organic phosphorus, hence, there was a net loss of total P. A coral without zooxanthellae was unable to remove net amounts of reactive P from solution, even at levels greater than the normal ambient levels in reef waters. Reactive P uptake was found to be light-sensitive, was highly temperature dependent, showed characteristics of Michaelis-Menton enzyme kinetics, and could be inhibited by arsenate. An active transport mechanism thus appeared to be involved in P uptake. The kinetics of net reactive P uptake were described by a Michaelis-Menton equation modified to include a correction for an efflux of reactive P going on at the same time. The mean half-saturation constant was 377 nM and the mean maximum rate of uptake was 293 ng-atoms P mg chl a^{-1} h^{-1}. D'Elia concluded that corals containing symbiotic algae are thus unable to obtain all their P requirements by means of reactive P uptake at typical environmental concentrations but that their ability to obtain part of the P requirements in this fashion may help them to flourish in water low in available P. This is probably further enhanced by the presence of mechanisms for efficient recycling of P within the symbiotic association.

Finally, Webb et al. (1977), in the paper previously discussed regarding nitrogen flux, briefly considered phosphorus along with nitrogen in the nutrient-flux measurements of *Holothuria atra* populations. They reported that the release of P followed the general rules in the literature for size–metabolism relationships.

TROPHIC TRANSFERS

Energy and nutrient transfer between trophic levels is perhaps the area of energy and materials flux which has been the least studied with respect to the amount of research that is required for a comprehensive understanding. This is an area of great interest for ecologists and for those concerned with the increasingly important area of reef management. A major effort would be required for such a comprehensive understanding. As with so many of the other topics discussed in this chapter, the first general effort in this area was that of Odum and Odum (1955). In addition to a description of trophic pathways and quantitative trophic pyramids discussed earlier, they made some preliminary attempts to quantify trophic transfers. While their work pointed the way for future research, it was hardly definitive; other researchers, so far, have been slow to take up the challenge.

Efforts since the Odums' study have directed attention to three main areas of trophic relationships. The greatest interest, cutting across these areas, appears to have been on transfers from the windward reef flats into the lagoon, with much less attention directed to transfers between trophic levels within the reef-flat subsystem. Aside from the relatively small-scale effort by Webb et al. (1977) to understand nutrition of the large populations of sea cucumbers on the reef flats (discussed previously), the greatest interest at Enewetak, as elsewhere, has been with the feeding relationships of the diverse fish community. Most of the interest has been either on the recurrent theme of "pseudoplankton" (relatively large algal fragments broken off from seaward reef zones and carried lagoonward) or on the role of coral mucus in trophic relationships, particularly those of the lagoon community. The mucus interest, at least, fits in with the general interest of many marine ecologists in the role of detritus and particularly of organic aggregates that first came to prominence in the late 1960s and carried over into the 1970s. It would be desirable to have a careful evaluation of the general framework of trophic relationships which could then be used to point out directions for future trophic research. A new overview paper such as that of Odum and Odum is needed because of recent understandings of marine ecosystems in general and reef ecosystems in particular.

Trophic Relationships of Fishes

A major early paper on trophic relationships of reef fishes was that of Hiatt and Strasburg (1960), who examined the feeding habits of 233 species. They distinguished

seven major groups of fishes: algal feeders, detritus feeders, scavengers, plankton feeders, carnivores, coral polyp feeders, and omnivores. Their algal feeders were divided into four categories: (1) those which subsist on unicellular algae (mullets and some blennies); (2) grazers, which crop very closely to substratum and ingest some of it along with the algae (surgeonfishes, damselfishes, gobies, blennies, triggerfishes); (3) browsers, which use cutting teeth for biting off algal fronds or filaments above the substratum and do not take in any of the nonalgal material (surgeonfishes, damselfishes, triggerfishes); and (4) incidental algal feeders, which feed primarily on other materials (butterflyfishes, wrasses, parrotfishes, gobies, puffers). The detritus feeders are represented by relatively few species (mullets, gobies, blennies). The scavengers included only the nurse shark. In addition to the manta ray, the plankton feeders included some round herrings, halfbeaks, silversides, damselfish, and wrasses. The carnivores included a large number and variety of fishes falling into five groups: (1) those feeding on fossorial fauna, (2) those feeding on benthonic fauna, (3) those feeding on mid-water fauna, (4) resident roving carnivores, and (5) transient roving species. The coral polyp feeders included browsers, grazers, and feeders on branching coral tips. Both facultative and incidental omnivores were recognized. Colin, in chapter 7 of this volume, considers the feeding relationships of fishes in greater detail.

Hiatt and Strasburg (1960) raised several points of interest in understanding trophic relationships of the fishes. These points have perhaps not been pursued sufficiently in subsequent research. They regarded benthic invertebrates as the chief organisms for converting particulate and colloidal organic material to animal protoplasm, with the energy and materials then reaching the fishes through predators on the invertebrates. Hence, they stated that an understanding of the primary producers and the trophic relationships of the higher organisms (i.e., fishes) is relatively well advanced in the reef ecosystem, "but there still remains to be known the role of the myriads of invertebrates which inhabit the reef."

Subsequent studies have continued to focus on the primary producer level and on the fishes, and the role of invertebrates is still relatively unknown. Hiatt and Strasburg pointed out that herbivorous species dominate the fish fauna of Marshallese reefs; this is a generalization which apparently applies to most reefs. Moreover, "It is still an enigma why the biomass of herbivorous fishes is so proportionately great on tropical reefs where the large seaweeds are not abundantly available, and so proportionately small along coastal shores in the temperate and arctic seas." This may be less an enigma than Hiatt and Strasburg thought, considering that algal productivity is high in reef ecosystems and that the rate of energy transfer through these producers can be high even with a small biomass. It is probable, however, that the role of algal turfs has been insufficiently appreciated and that these multispecies assemblages, which are visually unimpressive but are apparently subjected to heavy grazing pressure, have high rates of productivity even with their low-standing crops. (See Marsh, 1976, for further development of this point.)

Hiatt and Strasburg further pointed out that, among the fish fauna, surgeonfishes are the most important group in converting primary productivity into animal tissue; they convert large amounts of energy, whether or not they are efficient. This impression has generally persisted among reef ecologists. Hiatt and Strasburg also reported that all parrotfishes they examined had scraped coral polyps and that these animals may scrape smooth, algal-covered rocks as well. This was disputed by some later studies, which emphasized the grazing role of parrotfish rather than their ingestion of coral polyps, although the latter activity is generally acknowledged to occur to a greater or lesser extent. The Hiatt and Strasburg study has continued to be influential in shaping our thinking about reef ecosystems.

Hobson and Chess (1978) studied trophic relationships among fishes and plankton in the nearshore lagoon adjacent to windward islets. They found that feeding patterns differed sharply between day and night and were strongly influenced by current patterns. The adults of most diurnal planktivorous fishes were numerous in certain places where tidal currents were strong but much less numerous where such currents were consistently weak. Strong-current areas are rich and weak currents are poor in the major zooplankton prey of the fishes (e.g., copepods, larvaceans, and fish eggs). On the other hand, zooplankton-poor waters close to island lees and interisland lees are rich in reef debris; those fishes that could subsist in those areas were abundant. *Dascyllus reticulatus* was numerous in such environments, though less so than where currents were strong, and took algal fragments as an important but secondary part of its diet. Other species that fed largely on algal diets could be equally abundant in strong- and weak-current areas or more numerous where currents were weak.

Major nocturnal planktivores, in contrast to the diurnal feeders, were concentrated where the currents were weak but were relatively sparse where the currents were strong. These were found to be strictly carnivores that prey mostly on large zooplankers (large calanoid copepods, mysids, isopods, gammarid amphipods, postlarval carideans, and brachyuran megalops) which were absent in the nearshore water column by day. Such prey were reported to generally find conditions unfavorable where strong currents flow. Most of these found shelter on or near specific nearshore substrata during the day and entered the water column only at night; others were found to be in deeper offshore waters by day and moved inshore at night.

Overall, the pattern was clear to Hobson and Chess; most diurnal fish favored zooplankton rather than algal fragments. This pattern was somewhat at variance with the impressions that previous researchers had formed. The fish morphology that permits faster swimming is more developed in planktivores that swim farther from the reef; Hobson and Chess interpreted this as an adaptation to escape predators.

Smith and Paulson (1974) studied four transit times and gut pH's in two parrotfish species, *Scarus jonesii* and *S. gibbus*. They found that both species begin feeding around first light (reported to be about 07:30 hr) and continued feeding until about 19:00 hr, at which time individuals began aggregating in groups of 15 to 50 and then dispersed at last light (about 19:50 hr). They were seen feeding only on dead coral with its covering of filamentous algae, contrary to reports of Hiatt and Strasburg (1960) that these species feed on live coral. Smith and Paulson concluded that material ingested by the parrotfish at dawn is often evacuated within 4 hr and that food consumed at dusk passes through the gut in 6 hr or less. Such calculated transit times of 4 to 6 hr correspond to filling the gut at least twice a day. Feeding is intermittent.

In feeding *S. jonesii*, the anterior three gut regions (pyloric caecum, small intestine, large intestine) were found to be more acidic than seawater, with values of 6.8 to 7.5; the rectum (pH = 8.2) was not. In *S. gibbus*, all four regions of the gut (pH ranging from 6.4 to 7.5) are more acidic than seawater. Smith and Paulson emphasized that these were feeding fishes rather than those with empty guts. They concluded that $CaCO_3$ *may* dissolve in the parrotfish gut.

Reese (1977) considered the coevolution of corals and coral-feeding fishes of the family Chaetodontidae. He placed these butterflyfishes into one of three feeding categories: coral feeders, omnivores which feed on benthic invertebrates other than corals, and plankton feeders. The coral feeders may be obligative or facultative. At Enewetak, 10 of the 17 species studied were coral feeders (with four of these being obligate coral feeders), five were omnivores, and two were planktivores. Laboratory studies conducted in Hawaii showed that *Chaetodon trifasciatus* and *C. ornatissimus* preferred the coral *Pocillopora damicornis* over *Montipora verrucosa* over *Porites compressa*.

Nolan et al. (1975) examined the fish communities inhabiting two small nuclear test craters at Enewetak. They found the standing crops of herbivorous and carnivorous fishes to be 35.7 and 61.3 g m^{-2}, respectively, in LaCrosse Crater and 5.7 and 16.8 g m^{-2}, respectively, in Cactus Crater. This was higher than the 10.3 and 4.6 g m^{-2}, respectively, reported by Odum and Odum (1955) for their zone of large heads. In the two nuclear test craters, carnivores constituted 74.7% and 63.2% of the total biomass, but Odum and Odum reported herbivorous fish biomass to be four to five times that of carnivores. Nolan et al. estimated that 100 kg of goatfish alone might be harvested from the two craters every 1 to 2 days because there is continuous immigration.

The Role of Detritus

The role of detritus as a link between the reef flat and the lagoon was first noted by Odum and Odum (1955), who observed the transport of algal fragments from the back-reef zones into the lagoon. The next paper was by Marshall (1965), who believed that particulate matter carried off the windward reefs might constitute a substantial contribution to the trophic system within the lagoon. He stated that most detritus on cleared filters, sampled from water crossing the reef flat, appeared to be of plant origin, but he also noted the presence of amorphous organic aggregates. A lagoon sample from a coral knoll appeared to be similar to that of the reef flat. He found more detritus over the reefs and in the lagoon than in samples from the deep pass or seaward of the reef front. His values for combustible material trapped on glass filters were at least an order of magnitude greater than those of the earlier Odum and Odum study and sometimes almost two orders of magnitude greater. Ash-free dry weights from the lagoon averaged more than 0.1 g m^{-3}. Chlorophyll *a* values ranged from 0.08 to 0.14 mg m^{-3} in the channels, 0.21 to 0.33 on the coral–algal ridge, 0.15 to 0.39 in waters crossing the reef flats, and 0.16 to 0.61 in the lagoon. Ash-free dry weights were 0.04 to 0.15 g m^{-3} in the channels, 0.10 to 0.99 on the coral–algal ridge, 0.15 to 0.62 on the reef flats, and 0.06 to 0.22 in the lagoon.

Johannes (1967), in the first paper to focus on the role of coral mucus, further considered the ecology of organic aggregates and noted that these showed a markedly increased concentration as oceanic water crossed the reef and entered the lagoon. These aggregates consisted largely of coral mucus. Johannes estimated the export of mucus into the lagoon as 20 mg m^{-3} h^{-1}, or about 20% of the total reef production and 40% of total coral respiration. A few meters lagoonward of the drop-off at the back of the reef flat, organic aggregates were usually the only identifiable suspended objects in the water column; most of the algal fragments and sediment particles had settled out. In laboratory experiments, *Artemia* nauplii survived longer and grew faster in water with added mucus than in filtered seawater.

Coles and Strathman (1973) made further observations on coral mucus "flocs" and their potential trophic significance. They found that visible mucus flocs contain significant quantities of organic matter compared to microscopic suspended particle concentrations in surrounding water. Carbon to nitrogen ratios suggested that suspended mucus flocs are enriched with nitrogen compared to more recently secreted coral mucus or microscopic particulate organic matter. Freshly collected mucus, after drying, had organic contents comparable to other biological materials, 26% C and 3% N; caloric values were 3.95 gcal mg^{-1} (ash-free dry weight) for mucus collected from *Fungia scutaria*. Suspended mucus flocs collected on the lagoon side of the windward reef at Enewetak closely resembled mucus obtained from *Acropora* in the laboratory and contained algae, occasional protozoa, organic debris, and inorganics. Mucus flocs from different corals differed in C:N ratios and in the total quantities of organic C and N.

Gerber and Marshall (1974a, 1974b) considered the role of reef pseudoplankton in trophic systems of the lagoon. Gut analyses of *Undinula vulgaris* (a calanoid copepod), *Oikopleura longicaudata* (a larvacean), and several species of planktivorous fishes showed that detritus

amounted to 95% and 85%, respectively, of gut contents of the first two animals; chlorophyll was present in 2% and 6%, respectively, of the food mass. Planktivorous fishes were reported to consume, in addition to zooplankton, a substantial amount of detrital algal fragments. Fragments of the nitrogen-fixing blue-green algae *Calothrix* were abundant in the gut samples and were taken to be a primary contributor, both directly and indirectly, to lower C:N ratios in the lagoon. Chlorophyll *a* and phaeopigment levels in the lagoon waters were small, amounting to 0.098 mg m^{-3} and 0.085 mg m^{-3}, compared to total particulate C values of 20.5 mg m^{-3}. Waters over and behind the reef had lower levels of particulate C and N and higher C:N ratios than incoming oceanic water. Gerber and Marshall concluded that there is substantial input from the reef to the lagoon and that this input probably supports a more abundant zooplankton in the lagoon than would otherwise be the case. Gerber and Marshall stated that decomposition of algal fragments by fish digestion may be the first step in its transformation to a form that can be consumed by zooplankton.

In another study, Johannes and Gerber (1974) examined the import and export of net plankton by a portion of the reef-flat community by placing plankton nets (60-μ mesh) immediately upstream and downstream of the coral zones. Differences between these upstream and downstream nets showed a net import of organic C, N, P, benthic algal fragments, fecal pellets, and zooplankton by the coral zones. (However, analyses of small-volume water samples showed a net export of particulate C and particulate N for the whole transect.) Benthic algal fragments outweighed all other imported components combined; fecal pellets accounted for the rest of the detritus. Most algal fragments consisted of the red *Asparagopsis* or the blue-green *Calothrix*. Johannes and Gerber calculated that several thousand meroplankters were exported and several thousand holo- and meroplankters were imported daily by each square meter of reef surface. Some removal of algal fragments was due to settling out rather than feeding by animals. Johannes and Gerber concluded that reef communities are efficient traps of net plankton and that this may contribute to downstream changes in community composition and possibly to the limited width of interisland reef systems (through downstream plankton depletion).

Marshall et al. (1975) made additional observations on particulate and dissolved organic matter in reef waters. They reported that high concentrations of particulate organic carbon occur in the environs of reefs and may be attributed to the reef community itself. Changes in dissolved organic carbon (DOC) concentrations of waters flowing across reef flats are relatively small and inconsistent. The lack of distinct net increases in particulate organic matter (POM) of waters flowing across shallow reefs suggests that some of the released particles may be entrapped and consumed by the community. The composition of particulate matter is extremely varied, but there is always very little phytoplankton. As in most waters, particulate organic carbon (POC) levels are an order of magnitude less than DOC levels. Marshall et al. stated that there is an impressive increase of POC on rises and reef crests for all reefs studied, and there is a decrease in the ratio of DOC:POC from open ocean waters across reefs and into lagoons (changing from 103 to 33 for material trapped on glass filters).

The role of detritus in trophic relationships within the lagoon is considered further in Chapter 10 in this volume. The reader is referred to that chapter for a discussion of the magnitude and importance of inputs of detritus from the reef flats to the lagoon and for an integration of the various subsystems of the total atoll ecosystem.

ENEWETAK RESEARCH IN PERSPECTIVE

Although much pioneering work was done at Enewetak over the years, interest has now shifted to a number of other localities because of the shut-down of the Enewetak facility, the establishment of facilities elsewhere, and the rapid growth of reef research in the last decade. It is worthwhile to consider how the earlier Enewetak work fits into the broader context of more recent knowledge.

Advances at the community/ecosystem level have come in considering whole-atoll systems rather than simply reef flats, in examining temporal and spatial variations rather than relying on a restricted set of observations, and in more fully integrating nutrient fluxes into the total metabolic picture. Recent work is probably more striking for confirming and amplifying insights derived from Enewetak research than for reversing any major conclusions reached at that level.

Kinsey (1979, 1983) has considered "standards of performance" by reef ecosystems with respect to primary production and carbon turnover. He summarized metabolic studies and emphasized the considerable uniformity reported for reef flats from different latitudes and with differing biological makeup. The mean gross productivity for 16 studies was calculated to be 7.9 g C m^{-2} d^{-1} (standard deviation [S.D.] is 2.7), with a mean calculated 24-h respiration also of 7.9 g C m^{-2} d^{-1} (S.D. is 5.0). These are general values which are strikingly similar to the Enewetak-only values discussed earlier in this chapter. Further striking confirmation of the earlier Enewetak work comes from Kinsey's summary of P:R values consistently approximating 1.0 and his summary indicating that plankton metabolism is at least an order of magnitude lower than activity of the ecosystem as a whole. Furthermore, the Smith and Kinsey (1976) suggestion, based partly on earlier Enewetak work, of a bimodal model for calcification rates also appears to have been borne out by subsequent work at other localities. Hence, Kinsey (1983) suggested a generalized bimodal picture of (1) reef flats and all extensive, present-day metabolically active perimeter zones (whether an outer reef crest or the windward edge of a lagoonward patch reef) with a gross P of 5 to 10 g C m^{-2} d^{-1} and a calcification rate (G) of 3 to 5 kg $CaCO_3$ m^{-2} yr^{-1}, and (2) sand/rubble areas with contrasting rates of

1 g C m^{-2} d^{-1} and 0.5 kg $CaCO_3$ m^{-2} y^{-1}, respectively. The first mode is itself regarded as a composite and can be further subdivided. In particular, it may include areas of continuous coralgal cover and discrete heads with P = 20 and G = 10, where water depth and circulation are adequate. Kinsey proposed a "standard" reef flat with a gross P of 7 ± 1 g C m^{-2} d^{-1}, a P:R ratio of 1 ± 0.1, and a G of 4 ± 1 kg $CaCO_3$ m^{-2} yr^{-1}, where "reef flat" conforms to the concept of a fully developed (at or near present-day sea level), areally extensive (at least 100 m across), high-activity zone of the coralgal type.

Kinsey (1982) also considered comparative aspects of calcification rates and reef growth (accretion) between Pacific and Caribbean reefs and attempted to resolve what seemed to be discrepancies between the two oceans. He noted that the apparently higher rates in the Caribbean were based primarily on long-term accretion rates determined from stratigraphic methods and that most estimates in the Pacific were derived from short-term chemical changes in resident water masses. He concluded that there probably was a faster growth of Caribbean reefs during the Holocene epoch, with major factors being differences in sea level, tectonics, and wave energy. The particular combination of these factors in the Caribbean led to diminutive surface features and proportionately greater seaward slopes there, with wider expanses of reef flat and proportionately smaller seaward-slope areas in the Pacific. Kinsey further concluded that any interocean differences in the calcifying capacity of reef communities are small. Hence, additional research has served to put earlier Enewetak work into a broader context but has not drastically altered earlier conclusions resulting from Enewetak work.

One earlier impression probably arising from Enewetak research (e.g., Odum and Odum, 1955) should be modified. As pointed out by both Smith (1983) and Kinsey (1983), initial reports of high productivity of reef-flat communities led to the tendency to regard whole-reef systems or "coral reefs" as being one of the world's most productive ecosystems. However, if the complete system, particularly including the lagoon and extensive sand/rubble areas, is considered, the rates of production are much more modest. Kinsey (1983) tabulated published values of community metabolism for complete reef ecosystems and showed P (gross) ranging from 2.3 to 6.0 g C m^{-2} d^{-1}, G ranging from 0.5 to 1.8 kg CaCO m^{-2} yr^{-1}, and P:R ratios holding constant at 1 for the five studies. The distinction between particular reef communities and whole reef ecosystems is one which must be more carefully drawn in future studies.

Somewhat related to this point is the question of the metabolism of sediment communities, which comprise a substantial proportion of the whole system. Harrison (1983) studied this question by placing plastic domes over such communities at Enewetak and monitoring O_2 and CO_2 fluxes. He derived empirical respiratory quotient values of 0.8 and reported that more carbon is respired by the sediment community than is produced. He calculated that excess production exported from the windward reef flats was sufficient to support the metabolsim of these distinctly heterotrophic sediment communities. Both production and respiration showed a decline with depth. According to Harrison, "Biotic and functional comparisons between Enewetak and Kaneohe Bay, Hawaii, suggest metabolic and structural similarities between these physiographically disparate coral reef ecosystems." Thus, there is a recurring theme of similarities between reef processes at Enewetak and those in other seemingly different reef ecosystems.

Several important insights about nutrient availability had their origins at Enewetak but have been sharpened and extended by work at other localities. After the initial measurements of nitrogen fixation at Enewetak (Webb et al., 1975; Wiebe et al., 1975), there followed a number of other studies of this process at other localities (e.g., Crossland and Barnes, 1976; Burris, 1976; Capone et al., 1977). However, Szmant-Froelich (1983) pointed out that such measurements have generally been restricted to reef flats or back-reef areas and that denitrification (conversion of NO_3^- to N_2) has not been adequately measured in any reef environments.

Entsch et al. (1983), working on the Great Barrier Reef, also conducted research on nutrient availability. They found a large pool of nitrogen and phosphorus in carbonate sediments and in the interstitial waters of the surface layers of sediments. Nutrient concentrations were considered to be sufficient to allow high rates of uptake by epilithic algae. This is apparently an important recycling mechanism in reef systems.

Andrews and Muller (1983), building upon DiSalvo's (1971, 1974) idea of regenerative spaces, measured nutrients in a lagoonal patch reef of the Great Barrier Reef complex and studied rates of water percolation through the reef. Concentrations of NO_3^- and PO_4^{-3} in cavities on the vertical face of the reef were found to be significantly higher than in the surrounding water. Nitrogen export through tidal flushing of their patch reef was reported to be of the same order of magnitude as export from the Enewetak reef flat studied by Webb et al. (1975); this export was presumably supported by nitrogen fixation. The molar ratio of nutrient regeneration rates was calculated to be 140:2:7 for NO_3^-:NO_2^-:PO_4^{-3}; if NO_3^- and NO_2^- were lumped, the N:P regeneration ratio approximated 20:1.

Smith (1983) further sharpened our understanding of productivity and nutrient relationships in reef ecosystems by pointing out that the net productivity of the whole-reef system (rather than simply the reef-flat portion of the system) is low. He estimated it to be less than 100 mgC m^{-2} d^{-1}, or within about the same range as "new" production in open-ocean planktonic systems. As he and Szmant-Froelich (1983) pointed out, any net production in the ecosystem as a whole requires an input of new nutrients. Recycling of nutrients already in the system can support high gross production if the P:R ratio is exactly 1 and if the recycling is efficient. If recycling processes are not efficient then there must be an input of new nutrients

to maintain the steady-state system. With low net productivity and efficient recycling, whole reef ecosystems should not be expected to require large inputs of new nutrients. Hence, the apparent paradox of high-productivity reef systems in the midst of nutrient-poor waters, as perceived in the earlier studies, can now be viewed as not too surprising. Smith further argued that, since reef production is dominated by benthic plants with a C:N:P ratio of approximately 550:30:1 (Atkinson and Smith, 1983), they can produce more net carbon per unit of nitrogen and phosphorus availability than can planktonic systems with a C:N:P ratio of 106:16:1.

Atkinson (1981, 1982) challenged earlier ideas regarding the cycling of phosphorus in reef metabolism and argued that there is not a tight cycling of that element for a whole reef flat. However, because of a high advective flux of phosphate over most reef flats, the system can depend primarily on exchange with the water column for its nutrients; and only 10% of the PO_4^{-3} available to reef producers might be recycled through the water column. This challenge to earlier ideas has contributed to a continuing interest in the comparative roles of nitrogen and phosphorus fluxes in reef systems and the question of which of these elements is limiting to metabolism. For example, in a study of the whole lagoonal system at Christmas Island (Kiribati), Smith et al. (1984) argued that net metabolism of the system is limited by the availability of phosphorus. Ideas are developing rapidly, and additional work is likely to be reported in the near future. Crossland (1983) recently provided an overview of nutrients in coral reef waters.

Studies of individual populations of reef organisms have taken place at a larger number of geographic locations than have ecosystem studies. Work at Enewetak has not played the fundamental role for the former type of study that it has for the latter. Literature on the biology and ecology of individual populations is extensive and diverse. The reader is referred to the recent paper by Larkum (1983) for entry into the literature on productivity of plant populations, to the paper by Chalker (1983) for recent calcification studies of corals and other animals, and to the papers by Muscatine (1983) and Chalker and Dunlap (1983) for work on metabolism and production of corals.

SUMMARY

A number of significant single-investigator and team studies have been conducted at Enewetak and have contributed to a general understanding of reef ecosystems and to the development of methodology for studying such systems. Many of these studies have focused on the reef flats as the metabolically dominant subsystem of the whole atoll. The early study by Odum and Odum (1955), which attempted to relate structure and function in the windward reef-flat community, established a conceptual framework that is influential even today. Other important studies have focused on community metabolism, calcification processes at the ecosystem and organismal level, nitrogen and phosphorus cycling on the reef flats and in individual organisms, the trophic role of detritus, nutritional sources for corals, and the ecological relationships of reef fishes.

Table 1 summarizes most of the studies discussed in this chapter. Some of the highlights are reiterated in the following paragraphs.

Biological zonation is an important aspect of the structure of reef flats. Rates of community metabolism on such flats are high, with gross productivities of 6 to 10 g C m^{-2} d^{-1} for coralgal communities and 12 g C m^{-2} d^{-1} for algal-dominated communities; 24-h ratios of gross productivity to respiration approximate or exceed 1.0. Rates of calcium carbonate production on reef flats are also high, approximately 4 kg m^{-2} yr^{-1}, with little apparent difference between day and night; corals are a relatively minor contributor to the process at the level of the whole ecosystem. Rates of nitrogen fixation (and nitrogen export) on reef flats are again high, up to 1000 kg ha^{-1} yr^{-1}, and help account for the high productivity. Important nitrogen-fixing organisms include blue-green algae and bacteria. Studies at Enewetak suggest that internal phosphorus cycling within reef-flat communities is very efficient, with little exchange between the benthic biota and the water column; however, this conclusion has recently been challenged. The role of regenerative spaces has been examined in an exploratory way; such internal reef spaces probably deserve much more attention than they have received.

Various aspects of the biology of individual populations have also been examined at Enewetak. The primary productivity of the few algal populations that have been studied on a preliminary basis has been estimated at up to 2.3 gC m^{-2} d^{-1} for various species of *Halimeda*, with somewhat lower values for intertidal algal mats and calcareous red algae. The productivity of filamentous boring algae, originally thought by the Odums to be of major importance, is insignificant. Work conducted at Enewetak was the first to demonstrate that zooxanthellae from the tissues of corals and giant clams could release significant amounts of radioactively labeled photosynthate, which could presumably contribute to host nutrition. Other studies investigating the oxygen balance of corals and their enclosed zooxanthellae have indicated that at least some species have the capability of obtaining all their nutritional requirements from their symbiotic algae and that there can be sun and shade differences in the same species growing at different depths. Studies of the physiology of coral calcification have demonstrated light enhancement of this process (mediated by zooxanthellae), suggested the importance of active transport of calcium ions rather than diffusion, and found a marked temperature effect on the uptake of ^{45}Ca. Cyclic variations in the radial density (density banding) of coral skeletons were calibrated by examining the distributions of radionuclides in the skeletons, then used to estimate growth rates of individual colonies and later found to result from seasonal temperature differences. Nitrogen uptake in corals has been found to fit the active-transport model of enzyme kinetics for at least some forms

TABLE 1

Reef System Structural and Functional Characteristics That Have Been Measured at Enewetak

Characteristic	Quantitative estimate	Reference
Community net P (12-h day)		
Coralgal transect	4.8 g C m^{-2}	Odum and Odum, 1955
Coralgal transect	3.0 g C m^{-2}	Smith and Marsh, 1973
Algal transect	8.6 g C m^{-2}	Smith and Marsh, 1973
Community gross P		
Coralgal transect	10 g C $m^{-2} d^{-1}$	Odum and Odum, 1955
Coralgal transect	6 g C $m^{-2} d^{-1}$	Smith and Marsh, 1973
Algal transect	12 g C $m^{-2} d^{-1}$	Smith and Marsh, 1973
Gross P:R ratio (24-h)		
Coralgal transect	1.0	Odum and Odum, 1955
Coralgal transect	1.0	Smith and Marsh, 1973
Algal transect	1.9	Smith and Marsh, 1973
Organic CO_2 flux	$\pm$0.2 to 6 moles $m^{-2} d^{-1}$	Smith, 1974
$CaCO_3$ precipitation	4 kg $m^{-2} yr^{-1}$	Smith and Kinsey, 1976
$CaCO_3$ precipitation	$-$0.02 to .02 moles $m^{-2} d^{-1}$	Smith, 1974
Vertical reef accretion	3 to 5 mm yr^{-1}	Smith and Kinsey, 1976
Nitrogen export from reef flat	1000 kg $ha^{-1} yr^{-1}$	Webb et al., 1975
Mucus export from reef flat to lagoon	20 mg $m^{-2} h^{-1}$	Johannes, 1967
BOD, "internal sediments"	0.06 to 0.50 mg $g^{-1} h^{-1}$	DiSalvo, 1971
Net P, algal mats	0.6 to 2.15 g C $m^{-2} d^{-1}$	Bakus, 1967
Net P, *Halimeda*	Up to 2.3 g C $m^{-2} d^{-1}$	Hillis-Colinvaux, 1974
Net P, calcareous red algae	0.66 g C $m^{-2} d^{-1}$	Marsh, 1970
Gross P, calcareous red algae	1.5 g C $m^{-2} d^{-1}$	Marsh, 1970
Pavement O_2 evolution	Up to 5.5 $\times$ 10^{-3} ml $cm^{-2} h^{-1}$	Wells et al., 1973.
Pavement P:R ratio (24-h)	Up to 1.6	Wells et al., 1973
Photosynthate of pavement community released as soluble organics	50%	Pomeroy et al., 1974
Nitrogen fixation, algal-colored pavement		Wiebe et al., 1975
Upper intertidal	34 $\times$ 10^{-9} moles $cm^{-2} h^{-1}$	
Reef flat	55 $\times$ 10^{-9} moles $cm^{-2} h^{-1}$	
Ratio of nitrogen:phosphorus release in sea cucumbers		Webb et al., 1977
60-g animals	42:1	
1-g animals	25:1	
Dissolution of $CaCO_3$ by holothurian populations	2.5 g $m^{-2} d^{-1}$	Webb et al., 1977
P:R ratio (24-h), individual coral colonies		Wethey and Porter, 1976b

(This table continued on next page.)

TABLE 1 (cont'd)

Characteristic	Quantitative estimate	Reference
Shallow-growing (sunny and overcast days)	1.79, 1.44	
Deep-growing (sunny and overcast days)	1.81, 1.50	
Gross P required for R, individual coral colonies		Wethey and Porter, 1976b
Shallow-growing (sunny and overcast days)	31%, 45%	
Deep-growing (sunny and overcast days)	30%, 42%	
Linear growth rates, massive coral colonies		Highsmith, 1979
Favia pallida	5.7 mm yr^{-1}	
Goniastrea retiformis	5.8 mm yr^{-1}	
Porites lutea	7.6 mm yr^{-1}	
Mass growth rates, massive coral colonies		Highsmith, 1979
Favia pallida	0.82 g cm^{-2} yr^{-1}	
Goniastrea retiformis	1.16 g cm^{-2} yr^{-1}	
Porites lutea	1.07 g cm^{-2} yr^{-1}	
Kinetic parameters		Wethey and Porter, 1976b
Light response in coral *Pavora praetorta*		
Maximum rate, gross P (P_{max})	8.74 to 12.25 mg O_2 · mg chl a^{-1} h^{-1}	
Light level for half-saturated net P (K_m)	0.26 to 0.63 E m^{-2} h^{-1}	
NO_3^- uptake in coral *Pocillopora*		D'Elia and Webb, 1977
Maximum uptake rate (V_{max})	5.69 ng-atoms · mg-atom N^{-1} min^{-1}	
Half-saturation constant (K_s)	249 ng-atoms l^{-1}	
Threshold [NO_3^-] for uptake to occur	57 ng-atoms l^{-1}	
NH_4^+ uptake in corals (several spp.)		Muscatine and D'Elia, 1978
Diffusion	0.52 to 0.93 l · mg chl a^{-1} h^{-1}	
Active transport		
V_{max}	1.64 to 5.26 μmol · mg chl a^{-1} h^{-1}	
K_s	0.29 to 1.05 μg-atoms l^{-1}	
Reactive phosphorus uptake in corals		D'Elia, 1977
V_{max}	293 ng-atoms · mg chl a^{-1} h^{-1}	
K_s	377 ng-atoms l^{-1}	
Primary producer biomass	703 g dry wt m^{-2}	Odum and Odum, 1955
Primary consumer biomass	132 g dry wt m^{-2}	Odum and Odum, 1955
Carnivore biomass	11 g dry wt m^{-2}	Odum and Odum, 1955
Herbivore:producer ratio	18.9%	Odum and Odum, 1955
Carnivore:herbivore ratio	8.3%	Odum and Odum, 1955

(This table continued on next page.)

TABLE 1 (cont'd)

Characteristic	Quantitative estimate	Reference
Standing crop of herbivorous fishes in two nuclear test craters	35.7 and 5.7 g m^{-2}	Nolan et al., 1975
Standing crop of carnivorous fishes in two nuclear test craters	61.3 and 16.8 g m^{-2}	Nolan et al., 1975
Bacterial standing crops		
Sediments	10^4 to 10^5 cells · g dry wt^{-1}	DiSalvo, 1969
Water	80 to 200 cells ml^{-1}	Johannes et al., 1972
Standing crop of sea cucumbers *(Holothuria atra)* in zone of small heads	3 individuals m^{-2} 60 g wet wt m^{-2}	Webb et al., 1977
pH of reef flat waters	8.27 to 8.32	Johannes et al., 1972
Dissolved O_2 in reef flat waters	6.18 to 7.38 mg l^{-1}	Johannes et al., 1972
Alkalinity of reef flat	2.285 to 2.295 meq l^{-1}	Johannes et al., 1972
NH_3 in reef flat waters	240 to 287 nmol l^{-1}	Johannes et al., 1972
NO_3^- in reef flat waters	109 to 169 nmol l^{-1}	Johannes et al., 1972
Dissolved organic nitrogen in reef flat waters	1720 to 2145 nmol l^{-1}	Johannes et al., 1972
Particulate organic nitrogen in reef flat waters	157 to 210 nmol l^{-1}	Johannes et al., 1972
Reactive phosphorus in reef flat waters	169 to 174 nmol l^{-1}	Johannes et al., 1972
Organic phosphorus in reef flat waters	152 to 155 nmol l^{-1}	Johannes et al., 1972
Dissolved organic carbon in reef flat waters	1210 to 1230 μg l^{-1}	Johannes et al., 1972
Particulate organic carbon in reef flat waters	24 to 26 μg l^{-1}	Johannes et al., 1972
Suspended chlorophyll *a* in water column		Marshall, 1965
Channels	0.08 to 0.14 mg m^{-3}	
Coralgal ridge	0.21 to 0.33 mg m^{-3}	
Reef flats	0.15 to 0.39 mg m^{-3}	
Lagoon	0.16 to 0.61 mg m^{-3}	
Ash-free dry wt suspended in water column		Marshall, 1965
Channels	0.04 to 0.15 g m^{-3}	
Coralgal ridge	0.10 to 0.99 g m^{-3}	
Reef flats	0.15 to 0.62 g m^{-3}	
Lagoon	0.06 to 0.22 g m^{-3}	

(This table continued on next page.)

TABLE 1 (cont'd)

Characteristic	Quantitative estimate	Reference
Carbon:nitrogen ratio		Webb et al., 1975
Offshore waters	15:1	
Lagoon waters	6.6:1	
Composition of coral mucus		Coles and Strathman, 1973
Carbon	26%	
Nitrogen	3%	
Caloric value	3.95 gcal mg^{-1} (ash-free dry wt)	
Organic carbon in sediments, as % of total C	3%	Webb et al., 1977
Organic carbon in fecal pellets of sea cucumbers, as % of total C	10%	Webb et al., 1977
pH of parrotfish guts	6.4 to 7.5	Smith and Paulson, 1974

of that element, with the symbiotic algae implicated as the major agents in this update. Research on nitrogen cycling through reef-flat populations of sea cucumbers was reported to be a significant portion of total release by the whole community. Exchange of phosphorus between reef-flat organisms and overlying waters has been studied by several workers, leading to the general conclusion that exchange rates are slow and that there is a tight internal cycling in most (but not all) cases.

There have been a number of studies of trophic relationships and transfers, although no subsequent study has been as broad as that of Odum and Odum (1955). A number of fish groups, in particular, have been distinguished at various trophic levels. The role of detritus, both coral mucus and algal fragments, exported from the reef flats into the lagoon has been emphasized but not completely worked out, particularly with regard to its importance for various fish populations.

Overall, there have been a large number of studies of energy and materials flux at Enewetak, many of them of a pioneering nature which pointed the way to a general understanding of reef processes. However, the dominant theme must be the preliminary nature of what has been accomplished; a truly integrative understanding of reef processes probably lies a long way in the future.

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Chapter 10

Trophic Relationships in Enewetak Atoll

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INTRODUCTION

Some of the biologists who were attracted to Enewetak Atoll after the marine research laboratory opened have been studying species that are typical of reef environs and plentiful in this setting. Some have been interested in ecological features, particularly those of the well-developed windward reefs; and some, who have focused on the reef areas as an ecological subsystem, have been interested in the processes of the atoll as a whole.

We start by noting three contrasting environments in this large, but typical, atoll. First, there are the coral reefs and knolls, the former almost completely enclosing the atoll, the latter scattered through the lagoon and numbering over 2000. Then there are the open waters of the lagoon. Finally, there is the lagoon benthic environment (other than the coral knolls). In a real sense, and in comparison with the rest, the reefs and knolls are very productive, even though the oceanic waters surrounding the atoll are low in nutrients and organic food sources. The level of this productivity and the explanation (that the reef community dynamics involve rapid recycling rather than an enrichment from seawater), are discussed in Chapter 9, this volume, also in Odum and Odum (1955), and Johannes et al. (1972). In contrast it would seem that the lagoon waters are not productive; in fact, being extremely clear (often one can see the bottom to depths of 50 m and more), they give the appearance of being rather impoverished.

A Trophic Link Between the Reef and the Lagoon

Rather spectacular populations of fishes are evident in this dual setting of an impoverished lagoon and a productive, recycling coral reef seemingly low in net yield. This raises basic questions as to the food dynamics involved: how does the relatively closed reef system, together with the oligotrophic lagoon, support such consumer populations? Part of the answer is because the reef areas are not tight, unyielding environments as early studies suggested, and because there is an impressive flow of detritus, mucus flakes, algal fragments, and aggregated organic matter off the reef.

When the flow of matter off the reef was first reported, Marshall (1965) suggested "that [particulate] organic matter, including aggregates, transported in suspension from the reef to the mid-atoll areas, may constitute a substantial contribution to the trophic system within the lagoon." Soon thereafter Johannes (1967) made additional observations, noting a considerable flow of what he referred to as organic aggregates as well as detrital fragments streaming off the reef. His explanation, that the aggregates were the remnants of coral mucus, flaking off and flowing down-current from the rich reef environment, probably also accounts for some of the material Marshall had seen. Though Johannes provided additional quantitative information, the concept that organic particles flowing from the reefs might play an appreciable role in the lagoon trophic system remained a matter of conjecture.

Marshall had yet another idea as to a potential source of organic particles from off the reef, taking his lead from the publications by Baylor and Sutcliffe (1963) and by Riley (1963) in which they introduced the concept that dissolved organic matter in seawater might be aggregated into particulate food. The Baylor and Sutcliffe paper had demonstrated, in the laboratory, a mechanism that could explain their formation; namely, that dissolved organic matter in the presence of bubbles would aggregate and thus form particles. They commented on the possible importance of organic particles being produced by wave-induced bubbles at sea.

Reflecting on the crashing waves at the seaward edge of a typical coral reef, the streaming of bubbles in the path of flow across the reef, and the very high organic production of typical reef systems, Marshall envisioned a streaming of organic aggregates forming on bubbles or other nucleii. In observations on Hogsty Atoll in the Bahamas, he found that amorphous organic particles were indeed abundant in the lagoon but he could not establish a net

gain as water crossed the reef (Marshall, 1968). Thus this hypothesis concerning organic particle formation, attractive though it may be, remains unproven.

Whether one denies or argues that such a bubble-related aggregate formation mechanism is appreciable in the flow over a reef, there is no denying the earlier and continuing observations of detritus, mucus fragments, and other organic particles in the water flow toward the lagoon. In a very simple set of observations on corals held in shipboard tanks, Marshall (1972) showed that stimulation of corals by jets of seawater, intended to simulate the effects of breaking waves, did increase the output of organic particles. Qasim and Sankaranarayanan (1970) demonstrated that particulate organic matter greatly increased over the reefs of Kavaratti Atoll in the Laccadive Islands. During Project SYMBIOS, headed by Robert Johannes (Johannes et al., 1972) and with both Johannes and Marshall present, the research team was looking for striking examples of a rich mucus and aggregate flow, but a visible "marine snow" consisting of these small suspended particles was not as evident as that observed earlier by Johannes. Subsequently we have learned, from observations by Gerber and by John T. Harrison III (personal communication) that the appearance of "snow" varies from time-to-time and at differing sites behind the reefs.

Some quantitative information on such inputs, largely from Enewetak data, was summarized by Marshall, Durbin, Gerber, and Telek (1975). Also Johannes and Gerber (1974) report on plankton-net detritus in the reef flow at Enewetak, wherein they indicated a large percentage of algal fragments.

Such work provided the background for Gerber to take the necessary steps to explore the extent to which the detritus and various amorphous particles in the flow from the reef at Enewetak might be directly utilized by consumers in the lagoon. At first he focused on gut contents, analyzing a calanoid copepod, *Undinula vulgaris*; a larvacean, *Oikopleura longicaudata*; and seven species of the small pelagic fishes of the Enewetak Lagoon. For the two zooplankton species, he noted that detritus and amorphous particles predominated in the guts, while phytoplankton cells were present in only trace quantities. Though the small fish directly ingested reef detritus in the form of suspended algal pigments and fecal pellets, the bulk of the gut contents consisted of copepods and larvaceans. Coupling these observations suggests a food chain in which a base of detritus and aggregates is eaten by zooplankton (Gerber and Marshall, 1974a and b), which then can be eaten by the small fishes.

Later at Enewetak with the help of his wife, Mary, Gerber quantified the particulate food requirements of representative planktivores of the atoll system as he held them in the laboratory in containers filled with water from the lagoon. Ascertaining the particulate organic content of the water before and after feeding and subtracting fecal deposits, the Gerbers obtained quantitative data on material consumed and assimilated (Gerber and Gerber, 1979).

With this information and with the sampling of zooplankton populations carried out by Gerber while doing other work at Enewetak (Gerber, 1981), it was possible to approximate total requirements as noted in Table 1 (condensed from Gerber and Marshall, 1982). Since there were no assimilation assays for larvaceans to include in the table, it was estimated, on the basis of comparisons of the body content of carbon and nitrogen, that the requirements of this group are about one-sixth that of the small copepods (Gerber, unpublished data). Microorganism carbon requirements are based on summer respiratory rates of concentrated suspended particles from windward reef samples (Johannes et al., 1972). Winter rates were assumed to be about one-third the summer rates based on relative abundances (Gerber and Marshall, 1982). Nitrogen assimilation rates were estimated to be about one-eighth of the carbon requirements, interpreting a ratio of 8:1 from Vinigradov's (1953) chemical composition data.

TABLE 1

Assimilation Requirements of Particulate Organic Carbon and Nitrogen by the Major Primary Consumer Groups of the Pelagic Lagoon Environment*

	Winter 1972		Winter 1974		Summer 1974	
	C	N	C	N	C	N
Copepods	3.10	0.40	4.14	0.53	9.77	1.27
Pteropods	0.21	0.03	0.71	0.09	17.40	2.13
Larvaceans	0.28	0.04	0.37	0.05	0.97	0.11
Microorganisms	1.10	0.14	1.10	0.14	3.30	0.41
Rate of assimilation	[4.69]	[0.61]	[6.32]	[.81]	[31.44]	[3.92]

*Units are in mg m^{-3} d^{-1} (condensed from Gerber and Marshall, 1982).

Curious as to whether the reefs might supply an appreciable portion of these requirements, we noted that the windward reefs at Enewetak have a net transport of seawater into the lagoon amounting to 13.2×10^8 m^3 d^{-1}* during the month of June (Atkinson et al., 1981). This figure is multiplied by the quantity of particulate organic carbon (POC), 34 mg C m^{-3}, flowing off the reef [the average values for Enewetak samples collected on glass fiber and silver filters (Marshall et al., 1975)].† The

*Atkinson et al. (1981) give their data in terms of tidal cycles of 12 h 25 min. For quantities per day we simply double their data since none of the values are refined sufficiently to correct for the 50 min difference involved.

†Other workers (Simmons, 1979, and Westrum and Meyers, 1978) have commented on the utilization of such particulate organic carbon by the reef community and, in the Westrum/Meyers paper, quite a point is made of high POC at the reef crest with a rapid decline over the back reef. Our data (Marshall et al., 1975) does not show this marked difference between the reef and the back slope. For this discussion of input to the lagoon we use the back slope values.

product of these values divided by the volume of Enewetak lagoon, 420.5×10^8 m^3 (Atkinson et al., 1981), yields an effective reef input of particulate carbon of 1.07 mg C m^{-3} d^{-1} in summer. The effective reef input of particulate organic nitrogen (PON) is estimated to be one-sixth of the carbon rate, based on the C:N ratio of 6.6:1 for the particulate organic matter exported from the windward reef tract at Enewetak (Webb et al., 1975).

Because of the lack of entering data, values for the flux of POC and PON across the windward reef in winter are even more speculative. Though winter and summer are not differentiated as the data are presented by Atkinson et al. (1981), our interpretation of the lumped values and their range is that the currents across the reef, which as they point out are driven largely by surf, would be three times as great in winter when the trade winds prevail. Since the increased surf and current must cause a greater release of mucus from corals and of other detritus particles of reef origin, we have suggested that the reef input of C and N in winter is about three times greater than in summer, or >3 mg C m^{-3}. The potential reef input is appreciably increased if one speculates, quite reasonably, that at least some of the dissolved organic matter flowing off the reef (about three times that of the POC according to Marshall et al., 1975) is aggregated into particulate form available to consumers.

In winter such estimated inputs from the windward reef alone would seem to meet the estimated C and N requirement of the lagoon primary consumers. In summer, when reef inputs apparently are not as great yet consumer demands may increase, this input seems to fall far short of demand. Other sources that may be involved to meet estimated consumer requirements would be:

1. POC entering from other reef areas (i.e., from other than the windward sectors)
2. POC entering via the Deep Channel, the channel toward the Southwest, and through other passes
3. POC from coral knolls—there are 2300 of these with a total area of 9.8×10^7 m^2 (Emery et al., 1954)
4. Photosynthetic inputs
   a. From plankton
   b. From benthic macroflora
   c. From benthic microflora

Since Atkinson et al. (1981) report no net inward flow from across leeward reefs and through the passes, contributions via (1) and (2) probably are not very large. Also, since the depths of the crests of the coral knolls average 36 m below the surface and the flow is not great (2 to 4 cm s^{-1} according to Atkinson et al., 1981), it seems unlikely that there is a major input from that source. Among the photosynthetic inputs, the role of benthic macroflora must be minor since, as Gilmartin (1960) points out, such vegetation is not abundant. Similarly one can expect very little from benthic microflora in view of the lagoon depths of about 50 m, though it is possible that algae symbiotic in foraminifera, particularly in the shallows, contribute significantly. At Takapota Atoll, Sournia (1976) attributed high benthic productivity to such symbionts, and Lee (1978) suggests that this can occur in low light; however, there are no observations directly relating such an input at Enewetak.

This leaves photosynthesis by plankton as the likely major additional POC source. Unfortunately, there is only one set of determinations (Doty and Capuro, 1961), indicating a production of 5.76 mg C m^{-3} d^{-1} on a winter day. This scant information suggests that phytoplankton production may equal the combined inputs from the windward reefs and the other sources listed above. Furthermore, since Gerber and Marshall (1982) found that phytoplankton were more than twice as abundant in summer than in winter, it seems likely that such production is a major factor in meeting summer consumer requirements. (No consideration is given to dissolved organic matter generated from productivity within the lagoon since this would not constitute additional input but, rather, part of the production, release, and reformation processes taking place within that part of the system.)

To summarize, it appears that reef inputs constitute an important part of the lagoon trophic regime, especially in winter. Photosynthesis by the lagoon phytoplankton may be at least equally important, with summer inputs probably being the greatest. The average of consumer requirements in summer is not as great as Table 1 suggests since peaks in the abundance of pteropods and larvaceans (Gerber and Marshall, 1982) and concentrations of jellyfish described by John T. Harrison III (personal communication) are probably of short duration.

Comments on Organic Fluxes of the Atoll System as a Whole

The foregoing historical and narrative account of organic inputs and utilization in the lagoon deals with only one facet of the trophic relationships in the entire atoll ecosystem. Considered in a more comprehensive way, whether at Enewetak or elsewhere, the chief compartments of a reef and the adjacent shallow water ecosystem are the inputs from the

1. Surrounding oceanic waters
2. Outer reef slope
3. High reef
4. Knolls and patches in the lagoon
5. Overlying lagoon waters
6. Benthic environment of the lagoon *

These compartments, except for the oceanic waters, are lumped by some authors under the inclusive heading: "coral reef ecosystems."

It was mentioned previously that the inputs from surrounding oceanic waters are low. It is admitted, however,

*For some reef settings there are also extensive mangroves inshore of the lagoon or other coastal shallows, and these represent an additional input to the system; however, mangrove areas are not developed at Enewetak and generally are not extensive on atolls.

that for studies at Enewetak this has not been established from direct measurements but is assumed from general oceanographic considerations. Most of what we do know is inferred from sampling water as it comes in over the reef, already referred to in Chapter 9 where the observations of Odum and Odum (1955) and Johannes et al. (1972) are discussed. These observations could be misleading since they include an unknown net value for the uptake and the release from the outer reef slope. They are, however, compatible with the generalization that substantial coral formations can develop in relatively impoverished waters (see Lewis, 1977; Kinsey and Davies, 1979, for some of the factors that bear on this). One point that can be made is that, for an atoll system in an isolated setting surrounded by ocean depths, these surrounding oceanic waters are the only source of basic nutrients, except for the nitrogen fixation processes also referred to in Chapter 9

As mentioned earlier, the usual and plausible explanation for reef growth under these conditions is that the reef community, as a biological system, is uniquely adapted to the uptake of low nutrient concentrations and attains high gross productivity through recycling (e.g., Odum and Odum, 1955; Pomeroy and Kuenzler, 1969; and Johannes et al., 1972). It is often suggested that, in upwelling and other enriched areas where nutrient levels are higher, the success of competing ecosystems explains the general absence or poor development of reefs. Except that multiple responses and complications were involved, reef deterioration in Kaneohe Bay, Oahu, Hawaii, in the presence of nutrient-rich sewage effluents (also the recovery there after sewage diversion) seems to support this. [For discussions of the Kaneohe Bay story see Banner, 1974, and Smith et al., 1981.] Also, from fertilization experiments, Kinsey and Davies (1979) suggest that nutrient concentrations can suppress coral calcification. There does seem to be a positive effect from nutrient replenishment, however, since at Enewetak, as in most reef environments (Lewis, 1977), the growth is most luxuriant on the windward side where the greatest cross-reef flow occurs.

Unfortunately, very little has been done at Enewetak or elsewhere to provide a direct insight into the organic productivity of the outer reef slope. The nature of biological processes on the slope are probably not substantially different in kind from those of the high reef. Rates are undoubtedly reduced as light is attenuated with depth but, as various workers have shown, this reduction does not follow a direct linear relationship since there are some accommodations to reduced light. Some limited observations on calcium carbonate production on the slope (Smith and Harrison, 1977) suggest that, compared to the reef flat, the slope input is minor. Sheppard (1982) provides a comprehensive review of the little that is known about slope environments throughout the world.

As noted in Chapter 9, the high reef has been intensively studied. Generally speaking, gross productivity is extremely high; net productivity is not. Thus it is the limited net productivity of this region, plus that of the less productive outer slope and the input from relatively impoverished incoming oceanic water, that provides the sustenance described in discussing the trophic link from the reef to the lagoon.

The productivity input of the coral knolls of the lagoon, probably not great, and basic trophic relationships of the lagoon waters have been explored in the section on trophic links. As to the benthic environment, i.e., the lagoon floor, an impressive feature is the abundance of conspicuous consumer organisms. There are the callianasids (ghost shrimps), with mounds so closely spaced that there is often no level bottom between them, and sea urchins (six identified species) in varying densities up to 80 m^{-2} (Colin and Harrison, 1981). Harrison (1983) notes that more carbon is respired by the overall lagoon-bottom community than is produced there; thus we must assume that the bottom fauna must depend to some extent on fallout from the lagoon detrital and plankton complex.

This exercise, seeking to grasp the gross trophic relationships of the entire atoll system from fragmented information, probably serves primarily to offer a sense of what we do not know and need to learn. Even so, Enewetak observations tend to conform to a generalization, discussed by Kinsey (1979) largely from observations elsewhere, which suggest that, considered cumulatively, the reef components of such a system tend to be autotrophic, while the remaining environments tend to be heterotrophic. Whether this autotrophic/heterotrophic dualism balances out is not known. Referring to reef systems in general, Smith (1983) points out that we do not have a firm answer to this question. Reflecting on the gross picture at Enewetak, we think a balance does prevail, i.e., overall respiration equals or offsets overall productivity. If this were not the case, one would expect either an accumulation of organic matter on the lagoon floor, in contrast to levels <1% (John T. Harrison III, personal communication), or enriched oceanic waters down-current from the atoll. Unfortunately the waters flowing from the atoll have not been analyzed. Perhaps the lack of noticeable pelagic fisheries concentrated down-current from atolls suggests that enrichment there is not great.

Implications for Fishery Yields

Initially two considerations seem to imply a minimum fisheries potential, in spite of the very high gross productivity of the extensive reefs and knolls. On the one hand, many of the environments of the atoll system show little or no net production. Also, as suggested above, the whole atoll system seems to be in balance, with little or no excess productivity. On the other hand, certain considerations may offset this:

1. With systems so highly productive, even a small percentage net release can be appreciable. Furthermore, we have shown that such releases do occur and are being utilized by consumer food chains within the overall system.

2. Noting that marine fisheries commonly occur in regions that are in a climax or near-climax state, it is suggested that capture fishery harvests may involve tapping

the balanced (respiration equals production) systems or altering their intracommunity trophic structures to some degree, probably a bit of each. This raises a fundamental fisheries question of general application as well as for Enewetak: What level of harvests can be sustained through tapping an otherwise climax system or by altering it? Marshall has used the term "ecological sustainable yield (ESY)"* in referring to the harvest potential in this sense. (For a further development of this point see Marshall, 1979 and Marshall, 1985.)

Determining the yield potential as just discussed, i.e., through excess production, by tapping into the cycles of balanced systems, or by altering the systems, is not possible under present methodologies. Even if rates for these categories were well-known, the width of the confidence limits and the variability expected for such basic steps in the food web are of far greater magnitude than ultimate yields. Consequently, attempted calculations of the latter would be meaningless. Thus the only possibility for an appraisal of how much can be taken, i.e., the ESY, is to review actual harvest experiences. Summarizing data from reefs and adjacent shallows elsewhere, Marshall (1985) has suggested a generalized harvest potential of 4 to 5 metric tons km^{-2} plus miscellaneous gleanings from off the reef. While this may represent a norm, some reports show much higher yields. For example, for American Samoa, Wass (1980) indicated 27 tons km^{-2} while Hill (1978) indicated 12 tons km^{-2}. It now appears that the potential commonly may run well over 20 tons for some locales yet be even less than 1 ton for others (Alcala and Luchavez, 1982; Alcala and Gomez, 1985).

Though the research done to date at Enewetak has contributed very little to the yield question in any direct sense, the atoll could be used for further meaningful studies by experimentally fishing replicate knolls in the lagoon and critically observing the response to different fishing pressures. As in any climax environment, a properly managed harvest may serve as a culling process to the benefit of the system. Such observations at Enewetak, which has not been fished to any extent since early in the 1950s, could throw further light on this possibility. Hiatt and Strasburg (1960) offer a good foundation for such research in a publication rich in information on feeding habits and ecological relationships of Marshall Island reef fishes. Johannes, who was so involved in promoting basic ecological research at Enewetak, has become a leader in compiling useful life history information, often stressing insights gained from native fishermen (Johannes, 1978).

While the question of fisheries potential is a promising area for study, we would not wish to raise undue expectations but would close by quoting Kinsey and Domm (1974) who take a conservative view:

> Coral reefs generally have been found to exhibit a high turnover of carbon but a relatively small zero net gain. Thus, while they have typically one of the highest known naturally occurring levels of productivity, it is apparent that they cannot tolerate any heavy cropping. Removal of biomass not only involves the removal of carbon from the system, but other accumulated and recycling elements.

*This is not to be confused with the maximum sustainable yield (MSY) commonly used in fisheries and dealing with recruitment/growth/mortality patterns for single, or small numbers of interacting, species.

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Chapter 11

Terrestrial Environments and Ecology of Enewetak Atoll

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INTRODUCTION

Enewetak Atoll is a necklace of 39 coral islands surrounding a circular lagoon. The atoll is a coral limestone cap about 1400-m thick sitting on a pedestal of volcanic basalt rising abruptly some 5000 to 6000 m from the sea floor. Enewetak is about 50 to 60 million years old, having its birth in the Eocene of the Tertiary Period. It is noteworthy that during this time, sea level was about 50 m below the present level and that during the Wisconsin glaciation, about 20,000 years ago, the sea level may have been as much as 150 m below present sea level. What we do not know is to what extent vertical tectonic movements coupled with rates of coral growth match these sea water level changes. There is evidence that at one time the atoll was a raised coral limestone island. The physiography and geology of Enewetak are discussed by Colin and Ristvet, respectively, in Chapters 3 and 4 of this volume.

The dry land area of Enewetak Atoll is only about 2.5 mi^2, about 6.5 km^2, about 1600 acres, or about 647.5 hectares. The total land area is less than 4 m above sea level. The 39 islands which comprise this dry land area are distributed along the north, east, and south perimeter of the atoll (Fig. 1). A single, small island, Biken, occurs isolated on the west rim. The islands range in size and biotic diversity from extremely small patches of coral rubble colonized by sparse vegetation to the larger islands of Enjebi, on the north rim, which is triangular in shape and measures about 1.2 km^2 in size, and Enewetak, on the southeast corner, which is elongate and measures about 1.3 km^2 in size. The larger islands on the south rim of the atoll—Ikuren, Mut, and Boken—support a forest of mature coconut and *Pisonia grandis* trees and a correspondingly richer biota; however, these three islands together constitute only 0.45 km^2 of land area. It is important to note that the area of the lagoon, approximately 925 km^2, is about 138 times larger than the total area of dry land.

The terrestrial ecosystem of Enewetak Atoll is the result of the dynamic interaction between the biota associated with the small dry land area and physical parameters of the environment, especially the climate, soil, and groundwater. The shrubs and trees, man, birds, rats, and land crabs are among the more conspicuous elements of the terrestrial biota, whereas climatic events, the soils, and the availability of groundwater are the most important physical components of the ecosystem.

CLIMATE AND WEATHER

The climate of Enewetak Atoll is determined by its geographical location in the north central Pacific. The atoll lies well within the northeast trade wind area. The meteorological events affecting Enewetak and details of the climate are discussed by Merrill and Duce (Chapter 6, this volume).

With respect to ecology, there are a number of highly relevant aspects to the weather at Enewetak that deserve mention. There are two seasons, the dry season of approximately 4 months duration, December through March; and the wet season of approximately 8 months duration extending from April through November. All aspects of the weather are tied into this seasonal pattern.

Unvarying high temperatures, high humidity, moderate rainfall, steady easterly and northeasterly tradewinds, and partial cloudiness are all modulated seasonally. Even tropical storms and typhoons, which are otherwise unpredictable from year to year, occur more frequently in the wet season.

The average minimum temperature in the dry season is 23.6°C and 23.7°C in the wet season. The average maximum temperature in the dry season is 30.6°C and 31.8°C in the wet season. The variance around these means is very small (Table 1 in Merrill and Duce). The minimum temperatures occur at night or during storms, whereas the highest temperatures occur during the afternoon of the relatively few cloudless days, particularly during the months of August and September in the wet season.

Average temperatures, of course, are less important to organisms than are extreme temperatures which may exert

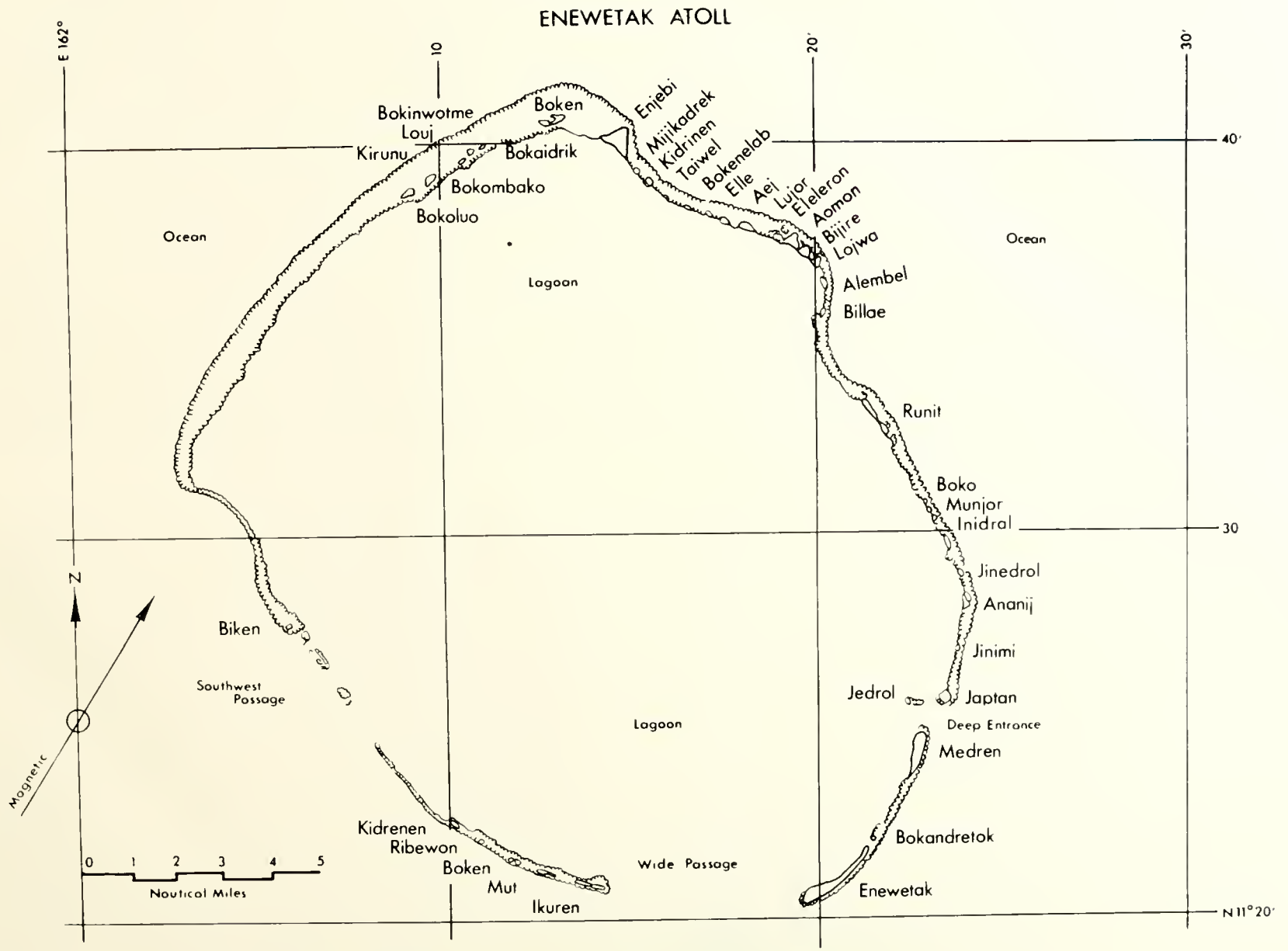

Fig. 1 Map of Enewetak Atoll with the Marshallese names of Islands.

direct physiological stress on them. Extreme temperature values for Enewetak are 21°C and 34.4°C, and these values are rare (Blumenstock and Rex, 1960).

These extreme temperatures, taken by themselves, probably do not impose severe physiological stress on any of the terrestrial organisms at Enewetak, providing water and shade are available. Seeking shade and the intake of water are well-known active behavioral processes of many terrestrial animals. Moisture and soil conditions determine the distribution and abundance of plants. Studies of the physiological ecology of terrestrial organisms were not undertaken at Enewetak.

There are, however, supporting observations. For example, *Coenobita* land crabs and especially *Birgus*, the coconut crab, discussed later, tend to be nocturnal or at least crepuscular in their activity. On dark, wet, overcast days, however, they are occasionally observed out foraging. Conversely, during the dry season they are more active on dark, humid nights of new moon or cloud cover, little wind, and brief rain showers.

Humidity is affected by temperature and moisture. It is maximal in the morning and decreases in the afternoon as temperature increases. It is higher during the wet season. Physiologically high humidity may have an ameliorating effect on high temperature through evaporative cooling, providing the organism can situate itself in a microhabitat of shade and exposure to wind. Unfortunately supporting data do not exist for terrestrial organisms at Enewetak.

Brisk, steady winds characterize the weather at Enewetak perhaps as much as the high, unvarying temperature and humidity. Trade winds blow from the east or northeast about 95% of the year. During the latter part of the wet season, August through October, wind direction is more likely to shift from the southeast around to the north. Wind speed is about 5.8 to 10.4 ms^{-1} (or 13 to 24 mih^{-1}). Winds are more brisk in the dry season and tend to weaken in the wet season. Again selective exposure to wind by an organism can ameliorate the effects of high temperature and humidity. Seabirds while nesting on land may position themselves to take advantage of wind direction (Lustick, 1984).

Partial cloudiness is the rule at Enewetak even during the dry season, when, however, the degree of cloudiness is more variable. The sky is seldom clear. Cloudiness decreases solar radiation and affects the duration of time a plant will be exposed to direct sunlight and, therefore, has a moderating effect on terrestrial ecology.

The average annual rainfall at Enewetak is 1470 mm. It is not distributed uniformly throughout the year. About 85% of it falls in the wet season starting in April and ending in mid-November. October is the wettest month. The remaining 15% falls in the dry season. There is considerable yearly variation. Needless to say, rain affects both temperature and humidity, and cloud cover is greatest during rainy periods. Situated in the extreme northwest, at 11°N latitude, Enewetak is one of the driest of the Marshall Islands. Kwajalein Atoll (9°N latitude) averages about 2400 mm, and the average annual rainfall at Jaluit Atoll (6°N, latitude) exceeds 4000 mm.

Perhaps the single most important aspect of rainfall in the terrestrial ecosystem is the replenishment of groundwater. The hydrography of Enewetak is discussed by Ristvet (Chapter 4, this volume). The larger islands of the atoll have a lens of fresh water of varying quality and volume. Probably the distribution and abundance of vegetation and related biota on the larger islands are directly related to the availability of groundwater. The correlation, however, is not possible due to drastic alterations of the vegetation resulting from activities during World War II and subsequent events at Enewetak.

Although on average the weather at Enewetak is both predictable and benign, at least in the general patterns described previously, there are two aspects of the weather which are remarkably variable and unpredictable. Both have profound effects on the terrestrial ecosystem.

First, wind and rain squalls, wind shifts, periods of little or no wind are of short duration and seem to occur almost at random. They are not detected within the larger weather pattern as measured periodically by conventional weather recording instruments. Nevertheless, these events are probably of great importance to terrestrial organisms in modifying the effects of high temperature, desiccation, humidity, and solar radiation. To my knowledge, measurements to substantiate this statement have not been made for the terrestrial biota of atolls.

Second, the occurrence and severity of tropical storms and typhoons are highly unpredictable. Tropical storms of greatest strength are called typhoons in the Western Pacific. Of eight tropical storms and disturbances which impacted Enewetak from 1959 to 1979, only one attained typhoon strength (Table 2, Merrill and Duce, Chapter 6, this volume). This was Alice, which struck Jan. 5 and 6, 1979. Three were tropical storms, whereas the remaining four were classed on the basis of their severity as disturbances or depressions. What is even more remarkable is that no weather disturbances occurred during the 7-year period 1959 to 1966 and for a 3-year period 1973 to 1975. Of the eight tropical storms and disturbances which did occur between 1967 and 1979, six occurred in the wet season with three of these occurring in October, the wettest month (no doubt these data are correlated), but two occurred in January in the dry season.

The severest of these, Alice in January 1979, caused the greatest amount of damage to the terrestrial environment of any storm that I observed over the 19 years, 1960 to 1979, that I visited Enewetak Atoll. Storm waves coming from the east and northeast washed over the entire north end of Enewetak Island (see frontispiece) carrying away vegetation and flooding the laboratory buildings. Wind speeds reached 145 km hr^{-1}. Strand vegetation of *Ipomoea* vines, *Lepturus* grass, and *Tournefortia* and *Scaevola* shrubs was either washed away by high seas on low-lying, small islets or denuded of leaves by the wind. Massive rearrangement of sand and coral boulders

occurred along the shore. The more densely vegetated islands such as Ikuren Island on the southwest rim of the atoll were greatly altered. Large *Pisonia* trees were stripped of their leaves and uprooted; *Tournefortia* trees were stripped of their leaves, many branches were broken, but relatively few trees were uprooted. Cocos palms were least impacted. The ability of palms to withstand typhoon-force winds deserves study. Bunches of coconuts and fronds were torn from the crowns, and, although a few trunks had broken, I recall no coconut trees being uprooted. By November 1979, the vegetation was making a remarkable recovery with new growth appearing everywhere from the remains of broken plants. Short green shoots covered the broken trunks and branches of *Tournefortia*. Similar rapid recovery of vegetation occurred following nuclear tests (Held, 1960).

Although surveys were not made, I suspect that the land crabs and rats were not greatly affected by the storm because they live in burrows and piles of debris, unless of course, these were close to shore. Held (1960) noted that land hermit crabs of the genus *Coenobita* survived the blast and heat effects of nuclear explosions. Apparently they were protected by the heavy shells of the marine gastropod *Turbo*. Most likely rats, if present, survived too in their burrows. The effect on insects and geckos which tend to live on the vegetation must have been much greater. Probably the birds were most severely affected by the storm. Fairy and noddy terns nesting in trees and ground-nesting seabirds would be greatly affected. A breeding colony of sotty terns on a sand spit between Ikuren and Mut Islands was completely washed away.

Overall, secondary ecological succession appears to be the result of typhoons on the terrestrial vegetation of an atoll. For example, in the early 1960s when I first visited Enewetak and began my work on Ikuren Island, the vegetation was a dense shrub-like growth, 3- to 6-m high of *Scaevola* and *Tournefortia* under a canopy of tall coconut palms. There were small meadows of *Lepturus* grass. Much of the vegetation had been cleared during the testing period in the 1950s, and what was evident was secondary growth. The coconut palms, neatly planted in rows, dated from the end of the 19th century when the Germans were organizing copra production in the Marshall Islands. In the 1960s there was a small stand of *Pisonia grandis* trees in the central part of Ikuren under the coconut tree canopy. This stand covering an area of about 1000 m^2 consisted of trees about 10-m high with trunks not more than 20 to 30 cm in diameter. Gradually over the years the *Pisonia* forest expanded until in the late 1970s it began to dominate the aging coconut trees (Fig. 2). A *Pisonia* forest seems to be the climax stage in the ecological succession of atoll vegetation (Lamberson's Stage V, Chapter 3, Volume II, this publication). The large *Pisonia* trees, however, are susceptible to storm damage. The wood is relatively soft, the canopy large, and the root system poorly developed in the shallow soil and rubble of the atoll. The trees are broken, uprooted, and blown over in tropical storms and typhoons, resulting in a return to an earlier successional stage. This is precisely what appears to have happened on Ikuren Island during Typhoon Alice in January 1979 (Fig. 3).

For further details and observations on ecological succession of vegetation on Ikuren and other islands of Enewetak Atoll, see Lamberson (Chapter 3, Volume II). What is very clear is that the vegetation has suffered repeated severe perturbation over the years, particularly the northern islands, but with time it begins to recover. Although diversity measures were not made, observations indicated that diversity is higher in the early stages, thereby supporting current disturbance theory (Loucks, 1970; Miller, 1982, Sousa, 1980).

SOILS

The calcareous soils of Enewetak Atoll are similar to those of other coral atolls (Fosberg, 1954; Fosberg and Carroll, 1965; Hammond, 1969; Jamet, 1982; Mason, 1960; Niering, 1963; Seru and Morrison, 1985; Stone, 1951, 1953; Trudgill, 1979; Wiens, 1962). They are relatively poor and immature consisting of limestone rubble, sand, organic litter, and humus in various mixtures. They have low moisture retention capacity.

If soils are defined in the broadest sense as the material on the ground surface in which plants grow, then atoll soils fall into five types:

1. Accumulations of coral rubble, mainly of stone size.
2. Unaltered coral sand and gravel.
3. Soils with a weakly developed A horizon with the color only slightly darker than the unaltered sand below but with no evidence of structural development. These soils are exemplified by the Shioya series (Stone, 1951).
4. Soils with a more developed A horizon that is deeper and darker in color than the Shioya type and with some structural development. These soils are exemplified by the Arno series (Stone, 1951).
5. Soils with an accumulation of raw humus on the surface and with a relatively deep A horizon as in the Jemo series (Fosberg, 1954). In the Jemo series, the accumulation of humus is specifically related to the presence of *Pisonia grandis* trees. There is an accumulation of phosphorus, often in the form of a cemented layer, believed by Fosberg to be due to the reaction between guano from the seabirds nesting in the *Pisonia* trees and the underlying coral sand. There is some evidence that such a humus-rich layer may develop under other suitable environmental conditions as well (Catala, 1957; R. J. Morrison, personal communication).

All of the soil types described previously would be classified under different names if conventional terms of soil taxonomy were used (Soil Survey Staff, 1975). Atoll soils, however, do not fall neatly into conventional classification, and students of atoll soils find the five types described previously to be more useful.

Studies of the soils were not conducted under the auspices of the Mid-Pacific Research Laboratory and, as a result, detailed analyses of the soils of Enewetak Atoll are

not available. Extensive radiological surveys were conducted in the northern Marshall Islands, including Enewetak, and provide information on the radionuclides in the soil, vegetation, and animals (Robison et al., 1981, 1982).

The two most common and troublesome radionuclides in the soils are cesium-137 and strontium-90 because they are picked up by plants, such as the coconut palm *Cocos nucifer*, and are concentrated in the leaves and nuts which may subsequently be consumed by man (Bastian and Jackson, 1975; Jackson and Carpenter, 1967). Radionuclides have a cumulative effect in the diet: the more you eat, the more you get. Surface material, soil, debris, and vegetation containing these and other radionuclides were collected, removed from the site of contamination, and entombed in a slurry of concrete in two atomic craters at the north end of Runit Island. Because of the transuranium nuclides, chiefly plutonium, at this former test site and because of the entombment of other radioactive materials on this island, Runit is permanently off-limits to humans. It is interesting to note that it took only a few years for seabirds to recognize Runit as an ideal nesting site. Seabirds returned to islands denuded by nuclear testing in less than two years (Held, 1960). The people of Enewetak prey heavily on birds and eggs, but they do not forage on Runit. In 1985, B. Ristvet (personal communication) gave a rough estimate of 10,000 birds nesting on Runit. He reported that the smell of guano was perceptible about a mile west of Runit in the lagoon.

Currently, at Bikini Atoll the United States government is making an effort to eliminate the radionuclides from the soil by means other than total removal of the contaminated soil. The soil is relatively poor in potassium, and to compensate, the plants pick up cesium-137. Adding potassium-rich fertilizers reduces the uptake of cesium-137. Although there is no clay in atoll soils which would serve to trap cesium, adding a mineral silicate such as mica tends to have the same effect. These findings offer hope that a solution can be found short of soil removal for Bikini Atoll. Fortunately, Bikini does not have the transuranium nuclides found at Enewetak which necessitated the extremely thorough cleanup of Enewetak Atoll.

From my observations at Enewetak, the A horizon varies in thickness from a few centimeters to 40 to 50 cm on the larger islands where it may be covered with a layer of decomposing vegetation. The soils are usually well drained and feel dry to the touch. Where they are poorly drained, for example in depressions where the water table is close to the surface, they have a wet sticky clay or muck-like consistency.

On Ikuren Island the A horizon is about 40-cm thick on the lagoon side. This part of the island is covered with a dense growth of coconut and *Pisonia* trees. Small meadows of grass, *Lepturus repens*, grow in open areas of the forest. Toward the ocean or south side of Ikuren, the soil grades into coral rubble mixed with organic debris but hardly any humus. This seems similar to the situation at Bonriki Island, Tarawa Atoll, described by Seru and Morrison (1985). The coconut and *Pisonia* vegetation gives way to *Scaevola* and *Tournefortia* as the soil gets coarser. The coral rubble becomes increasingly coarse until it ends abruptly on a steep seaward berm of unconsolidated coral rubble. The limestone rubble and sandy soil are typically gray in color due to the blue-green algae, *Brachytrichia quoyi*, which may be important in nitrogen fixation (Niering, 1963; Wiens, 1962).

According to Trudgill (1979), there are three primary sources of the soil of Aldabra Atoll:

1. Mechanically derived carbonate fragments
2. Chemically derived solution residues
3. Leaf litter

The composition of the vegetation and the phosphates and nitrates derived from fecal material of birds, crabs, and rats—all more abundant where there is more vegetation—have considerable influence on the nature of the atoll soils where the influence of organic materials is especially significant. This is an important observation because it means that the soil of an island such as Ikuren, which has had good vegetation cover during the recent past, should be richer than that of Enjebi and other islands on the east and north rim of Enewetak, where the vegetation has undergone much disturbance during the past 40 years.

Soil is a precious terrestrial resource. In the atoll situation, the influence of organic material is all important. It not only carries out the normal role of soil organic matter in storing and recycling nutrients, but it is also the major moisture storage component in the soils, since coral sand and rocks have an extremely limited moisture storage capacity. The fertility of atoll soils, therefore, is almost entirely dependent on the content of organic matter (Seru and Morrison, 1985). Every effort must, therefore, be made to protect the organic-rich layers from erosion and conserve them through cover of native vegetation.

TERRESTRIAL BIOTA (EXCLUDING MAN)

The terrestrial biota and ecology of Enewetak were not studied as thoroughly as the marine ecosystem. From the inception of the laboratory, the emphasis was placed on marine organisms. The historical reasons for this are not altogether clear (Helfrich and Ray, Chapter 1, this volume; Hines, 1962). In part it was because of the magnitude of the marine environment when compared to the terrestrial one and because there was an early concensus that a great deal more was known about the terrestrial organisms than about the multitude of unfamiliar marine organisms. In any event, the opportunity to conduct research on a tropical coral atoll apparently was much more appealing to marine biologists than to other scientists. As a result far fewer studies were made on the terrestrial biota and ecosystem.

We lack comprehensive, long-term studies of the plants of Enewetak. What we do know has been summarized by Lamberson (Chapter 3, Volume II). Ecological processes have not been studied in the terrestrial ecosystem of Enewetak. Other than species lists, we know very little

Fig. 2 a, Ikuren Island looking west. The coconut and *Pisonia* forest is in the central part of the island. *Scaevola* and *Tournefortia* scrub vegetation is evident in the foreground; b, Coconut trees and sprouting nuts on Ikuren Island. Clumps of *Lepturus* grass are seen growing on the coral rubble soil; c, Lagoon beach of Ikuren Island. At night the land crab *Coenobita perlatus* forms courtship aggregations on this beach, and it is across beaches such as this that the glaucothoe of *Birgus* and *Coenobita* emigrate from the sea to the land. [Photographs by E. S. Reese.]

Fig. 3 a, Typical beach vegetation consists of *Lepturus repens* grass, the flowering morning glory vine *Ipomoea pes-caprae*, and the single whorl of leaves and small white inflorescence of the shrub *Tournefortia argentea*; b, The interior of the forest on Ikuren Island in the early 1960s when the *Pisonia grandis* trees were still small in the foreground. Note the sprouting coconuts. [Photographs by E. S. Reese.]

about the herptofauna and insects of the atoll. We know essentially nothing of the role of the soil organisms (Maguire, 1967). What little is known of the birds is summarized by Berger (Chapter 13, Volume I, and Chapter 29, Volume II, this publication). We lack studies on the behavioral and physiological ecology of the seabirds which play such a profoundly important role in energy and nutrient transfer between the marine and terrestrial ecosystems.

Only the land crabs and rodents were studied thoroughly over a number of years. The research on the rats and mice of Enwetak is described by Jackson et al. in this volume (Chapter 12).

Land Crabs

Land crabs and birds are the most conspicuous animals of the atoll. Of the land crabs, those belonging to the Family Coenobitidae, the land hermit crabs, are the most conspicuous. Bright red to brownish red adult *Coenobita perlatus* are found on most of the islands. Usually the adults are found in *Turbo* shells, while the younger, smaller crabs

inhabit a greater variety of shells. Four other species of *Coenobita* are present, but they are small and less colorful. The legendary coconut crab, *Birgus latro*, the largest living terrestrial invertebrate known, is nocturnal. It prefers dense vegetation and is common only on the southwest islands of the atoll from Ikuren to Biken. The brachyuran land crab, *Geograpsus crinipes*, occurs but is secretive, preferring a habitat of decaying vegetation in the forest. In contrast, their relatives, especially the grapsid crab, *Grapsus tenuicrustatus*, and the ocypodid ghost crab, *Ocypode ceratophthalma*, are active and conspicuous scurrying over the intertidal beachrock or digging their burrows in the beach respectively. These species are semiterrestrial only and are not considered here.

At Enewetak, the behavioral ecology and life history of the coconut crab, *Birgus latro*, were studied extensively by Helfman (1973, 1977a, b), Reese (1965, 1968), and Reese and Kinzie (1968); and the behavioral ecology of *Coenobita* spp. was studied by Held (1960), Page and Willason (1982, 1983) and Willason and Page (1983). Osmoregulation, an important aspect of the physiological ecology of land crabs, was studied by Gross (1964) and aerial respiration by Cameron and Mecklenburg (1973). Elsewhere land crabs were studied recently at Aladabra Atoll, Indian Ocean, by Alexander (1979) and in the Mariana Islands by Amesbury (1980). There is an excellent account of the role of land crabs in the atoll ecosystem in Wiens (1962). The discussion which follows is based on these publications, literature citation therein, and my own observations between 1960 and 1979.

Land crabs are tied to the sea for two reasons. First, they release their fertilized eggs into the sea where they go through typical crustacean larval stages in the plankton. Second, their blood is isosmotic with seawater, and periodically they must have access to seawater to maintain this condition. They are, nevertheless, surprisingly euryhaline (Gross, 1964). Land crabs are scavengers on terrestrial organisms, so most of their food presumably is less salty, that is hypoosmotic, to their body fluids.

Birgus is extremely secretive and must be observed at night with infrared viewing equipment if its behavior is to be studied. Helfman (1977b) observed copulation in *Birgus* on land, and at this time the spermatophore is transferred to the female. It is not clear when fertilization actually occurs. The eggs are carried by the female on her pleopods for about 3 weeks. In the case of *Coenobita perlatus*, males tend to cluster around females on the beach at night. They tumble and fight with one another trying to gain access to the female. Presumably they are attracted to her through chemosensory channels, but vision plays a role too as rocks on the beach are also approached and explored by males. Eventually one male wins access to the female, both crabs partially emerge from their shells, ventral sides together, and the spermatophore is transferred to the female. She then proceeds into the water. It appears likely that a ripe batch of eggs are hatched at this time, the larvae are released, a new batch of eggs are extruded to the pleopods, and fertilization occurs. Verification of these events is necessary. Matthews (1956) was unable to find adaptations for terrestrial fertilization in either *Birgus* or *Coenobita*.

At Enewetak, *Birgus latro* females carry eggs from about April through August. Initially the eggs are deep purple red. As they develop on the pleopods of the female they gradually turn lighter until just before hatching they are light, translucent brown. The dark eyespots of the embryos are visible at this time. With remarkable timing, the female crab goes to the shore, walks out into the water, flexes her abdomen repeatedly, and the thousands of eggs hatch into free-swimming, first-stage zoeae larvae.

The larvae go through three more free-swimming stages, four zoeal stages in all, before metamorphosing into a postlarval stage called a glaucothoe. Reese and Kinzie (1968) provide diagnostic features to distinguish the glaucothoe of *Birgus* from those of other *Coenobita* species.

The glaucothoe is a critically important life history stage for these crabs. It is at this time that they carry out a unique behavioral program. The glaucothoe, about 4-mm long, settles to the bottom and begins to look for a small, empty gastropod shell. It explores the shell using typically hermit crab patterns of shell exploratory behavior (Reese, 1962, 1963). Then, with its newly acquired shell, the *Birgus* or *Coenobita* glaucothoe crawls out onto the land (Reese, 1968; Fig. 4). Shortly thereafter it undergoes a second metamorphosis to a miniature crab. The abdomen becomes asymmetrical in typical hermit crab fashion. These tiny creatures are found in the high beach zone usually under rocks or debris. The wrack of the high-tide line is a good place to look for them.

As they grow, they move inland. *Coenobita* crabs never give up the behavioral characteristic of living in empty gastropod shells, and, indeed, the availability of sufficiently large shells may limit the population of large adult crabs. At Enewetak, *Turbo argyrostomus* is the shell most used by large coenobitid crabs. Many of the shells are broken and worn and appear to have been in use for a long time. The shell must be able to hold a small reservoir of water apparently to keep the reduced gills and vascularized surface of the gill cavity (sometimes called a pseudolung in land crabs) moist. Close examination of empty shells found in the jungle reveals a smooth, round hole in the ventral whorl of the shell making it unsuitable for holding water. The hole seems to be caused by solution from within rather than wear from without.

The coconut crab *Birgus* lives in shells only when it is small. Crabs reared in the laboratory abandoned shells after about 2 to 3 years when their carapace measured 1 to 2 cm in length. During this time they were nocturnal and secretive. Small crabs of this size are extremely difficult to find in the forest on islands such as Ikuren. What is important to note is that *Birgus* stop living in gastropod shells at a very small size when suitable shells are still available to them. Reports of large coconut crabs living in shells or even in coconuts are misidentifications. In most cases that I am familiar with, the crab is *Coenobita brevimanus* which, like *Birgus*, is often bluish in color.

Fig. 4 a, The glaucothoe of the coconut crab *Birgus latro* emigrating from the sea to the land; b, The same on a U. S. dime for scale; c, A large adult coconut crab *Birgus latro* sitting among coconuts. The carapace may attain a width of about 15 cm, and the legs may extend to nearly 1 m; d, An adult *Coenobita perlatus* in a worn *Turbo* shell sitting in the crouch of a *Tournefortia* tree. [Photographs by E. S. Reese.]

Both *Birgus* and *Coenobita* are opportunistic scavengers. They eat animal and vegetable remains as well as fruits and probably bird eggs. I have seen them feeding on dead birds and fish on the beach and dead rats in the forest, and they are readily attracted to almost any kind of human food. *Coenobita* quickly walk upwind to a garbage dump and may even walk into the warm coals of a campfire to retrieve food. *Birgus* is more secretive and prefers to take food to its burrow.

The crabs do climb trees for unknown reasons; however, *Coenobita* especially climb into *Scaevola* and *Tournefortia* shrubs in which noddy terns are nesting, and model eggs were found with scratch marks on them. Coconut crabs climb coconut trees, but they have never been observed by Helfman or Reese to cut down coconuts. They are unable to open green coconuts. They do, however, open brown coconuts on the ground. Usually the nut is completely husked, and the reddish brown fiber is often conspicuous at the entrance to a burrow (Fig. 5). The crab apparently pierces the soft eye of the coconut, the one through which the young plant will emerge, and then with its powerful cutting claw cuts open the nut. To my knowl-

Fig. 5 a, A burrow of the coconut crab, *Birgus latro*. Note the partially shredded coconut and above it the fiber at the entrance to the burrow; b, Land crabs *Coenobita perlatus* are active scavengers. They are abundant on Ikuren Island. [Photographs by E. S. Reese.]

edge, the entire sequence of events has not been observed. There are a number of questionable accounts in the literature. It is important to note that the broken line on old nuts found in the forest always passes through one of the eyes. This is not true of the clean break made by a man with a machette. Rats can gain access to nuts by gnawing through the tough fiber and into the soft eye of the nut. Rats do not shred the fiber from the nut, and, therefore, nuts opened by rats are readily distinguishable from those opened by crabs. Rats can gnaw into green nuts in the crown of the tree. *Coenobita* are unable to open coconuts and must rely on what is left by *Birgus* and rats.

The population of coconut crabs on Ikuren Island was studied periodically from 1960 to 1976 using tagging recapture methods by Reese, Helfman, and their colleagues. These data will be part of a monograph on *Birgus latro* which is in preparation. The population size on Ikuren ranged from a low of 300 crabs estimated in April of an exceedingly dry season to a high of about 1200 to

1400 crabs during the rainy wet season. Because of the life history characteristics of *Birgus* emigration, immigration, natality, and morality are not considered to affect these estimates. Adult crabs cannot move between islands. Small, young crabs are secretive, slow growing, and not numerous in the data. Large adult crabs are estimated to be 30 to 40 years of age. Therefore, the differences in population estimates are postulated to result from foraging behavior. The best explanation of the data is that during ideal conditions of moisture and lush vegetation, the crabs forage every night, while under adverse, dry conditions, they forage only every third to fourth night.

The ratio of females to males is nearly even. Males are larger than females. Crabs are solitary. Small crabs defer to large crabs when feeding.

Four species of the genus *Coenobita* occur at Enewetak. *Coenobita perlatus* is the most abundant and conspicuous species. The large red adults remain in the forest during the day but go to the beach at night to forage, to replenish the water in their shells, and to reproduce. They prefer dark nights. A full moon tends to inhibit their activity. Small *C. perlatus* occur at all times closer to the beach; and their numbers are associated with the amount of debris and cover present on the beach. They may be tied closer to the beach by osmoregulatory demands. *Coenobita rugosus* is common too, and both large and small individuals tend to occur farther inland. They are less common on the beach, and these were generally females engaged in releasing their larvae into the sea. *Coenobita brevimanus* is not common. It tends to occur deeper in the forest often closely associated with *Birgus* and indeed has been confused with *Birgus*. Gross (1964) suggested the *C. brevimanus* may be more dependent on fresh water for shell reservoir replenishment than the other two species. *Coenobita cavipes* is rare. The availability of suitable, empty gastropod shells appears to limit the population of crabs on smaller islands such as Bokandretok when compared with larger islands like Ikuren.

Coenobitid crabs are scavengers like *Birgus*, and Page and Willason (1983) demonstrated that they play an important role in reducing carrion and thereby potential fly breeding sites. They also feed on fruits, flowers, roots, and seedlings of a wide variety of plants.

Land crabs play an extremely important role in atoll ecosystems. Alexander (1979) and Fosberg (Wiens, 1962) observed that crabs carried seeds from the beach into their burrows, thereby effectively planting them, providing they were not eaten. They also noted that on atolls where *Coenobita* scavenged and removed carrion, flies were not abundant, whereas on atolls where *Coenobita* were scarce, flies were common. Flies lay their eggs in rotting organic material, especially carrion. In addition, the burrowing behavior of land crabs tends to mix and aerate the rubble and poor soil of the atoll.

On uninhabited islands adult *Birgus latro* reign as the dominant terrestrial animals. They are vulnerable to rats and insects at time of molting only, but this is done underground affording some measure of protection. Man is the principal predator on adult coconut crabs and probably adult *Coenobita* as well in the atoll ecosystem. Where human populations are high, crab populations, especially populations of *Birgus*, considered a delicacy, are low.

Rats

Although the biology of Enewetak rodents is treated elsewhere in this volume (Chapter 12, Jackson et al.), it is important to attempt to evaluate the impact of rodents on the atoll ecosystem. In general, rats are considered destructive to island ecosystems (Smith, 1969; Wodzicki, 1969, 1972). They are a major problem in coconut and sugar cane plantations. The least offensive is the Polynesian rat, *Rattus exulans*, considered a commensal with man; it probably accompanied, most likely as a stowaway, the early Micronesians on their voyages of discovery. The roof rat, *Rattus rattus*, and the Norway rat, *Rattus norvegicus*, are larger and do more damage. Fortunately, at the time Jackson and his colleagues conducted their surveys (1964 to 1978) only the roof rat was present at Enewetak.

Temme (1982) examined the stomach contents of 602 Polynesian rats collected in the northern Marshall Islands during the wet season, October and November 1978, including 243 from five islands of Enewetak. By estimated volume, about 98 to 99% of the diet of *R. exulans* is of plant origin. The remaining 1 to 2% is animal matter, principally insect remains. It should be noted, however, that the cellulose of plant material and the chitin of insect parts are more readily detected in stomach contents than, for example, the remains of a bird's eggs. Temme noted that those islands which were free of rats had the largest bird populations.

At best, rats may contribute to the atoll ecosystem by digging burrows, thereby helping to aerate the soil, and by feeding on carrion, including human excrement, thereby reducing the potential breeding sites for flies. At worst, because they enter human habitations, they may be vectors for disease, they compete with man for plant food, and, in all probability, they attack the eggs and young of nesting seabirds. The latter may be their most destructive role because seabirds play such an important role in providing organic replenishment of atoll soils. Seabirds are perhaps the single most important group of organisms providing an energy bridge from the marine to the terrestrial atoll ecosystem.

MAN AND THE ISLAND ECOSYSTEM

Carrying Capacity

Man is the dominant biotic component of the terrestrial ecosystem. This is especially true for small, isolated, self-sustaining ecosystems such as islands. Indeed, the concept of carrying capacity of Pacific islands for human populations is the subject of considerable interest and concern (Bayliss-Smith, 1975; Carroll, 1975; Kirch, 1980; Kiste, 1974). The consensus is that island populations had reached their full potential size before contact with Europeans. In the Marshall Islands, ownership of land is of

great importance both economically and socially (Kiste, 1974). Carroll (1975) refers to "homeostasis in the precontact populations" in his study of the population of Nukuoro Atoll. It is probable that Pacific islanders were well aware of the dangers of overpopulation, and homeostatic population controls were actively practiced. Carefully controlled infanticide was a primary mechanism (Bayliss-Smith, 1975).

Taro, *Colocasia esculenta*, is regarded as the essential staple in estimating carrying capacity because it is the only substantial source of starchy carbohydrate. Abundant protein from the sea seems to have been of less importance. In almost all cases, European contact resulted in sharp declines in island populations due largely to disease.

Little is known of the populations of the Marshall Islands, much less individual islands, before European contact (Hezel, 1983; Howe, 1984; Kiste, 1974), but it is estimated that at the time of European contact in the mid to late 1800s the population of all the Marshall Islands was about 10,000 inhabitants. Today there are about 35,000 inhabitants.

With respect to Enewetak, it is interesting to ask what the population size was in the past, especially before the major disturbances of World War II. In the late 1800s Hager (1889) reported that there were about 40 inhabitants living on Enewetak, probably representing a severe post-European contact decline in the atoll's population. By 1896, Irmer reported 60 natives on the atoll. According to a British Naval Intelligence publication of 1945 (Naval Intelligence Division, 1945), the population in 1935 amounted to 81 natives and 13 Japanese. This figure is at variance with a figure of 121 inhabitants in 1930 given by Emery et al. (1954). Kiste (1974) provides comparable figures for nearby Bikini Atoll. Although Japanese traders lived on the atoll at this time and copra was being produced, the Japanese administration was based in Ponape, and in all likelihood most of the sustenance of the native population was based on the indigenous food resources of the atoll. At the end of World War II, it is said that there were about 130 Enewetak people living on Enjebi Island where they had been moved by the Japanese. Other figures are 136 and 141 people in 1944, at which time they were again living in their two traditional communities located on Enewetak and Enjebi Islands. I am unable to verify these figures with references. According to R. C. Kiste (personal communication), there were 141 people in the Enewetak community in 1947. Based on all these figures, it appears that the carrying capacity of Enewetak Atoll is about 125 to 150 human beings.

The food web, energy-flow pattern for the Enewetak ecosystem showing major food sources for man, especially from the terrestrial environment, is shown in Fig. 6 and is based on dietary information from Domnick and Seelye, 1967; Muri, 1954; Naidu et al., 1981; Niering, 1963; Robinson et al., 1980; Wiens, 1962. The diet pattern depicted is that of a community (Naidu et al., 1981; Robinson et al., 1980) which is characterized as follows:

1. Maximum available local foods
2. Highly depressed local economy—living within income provided by selling copra
3. Low population
4. Little or no ability to buy imported food

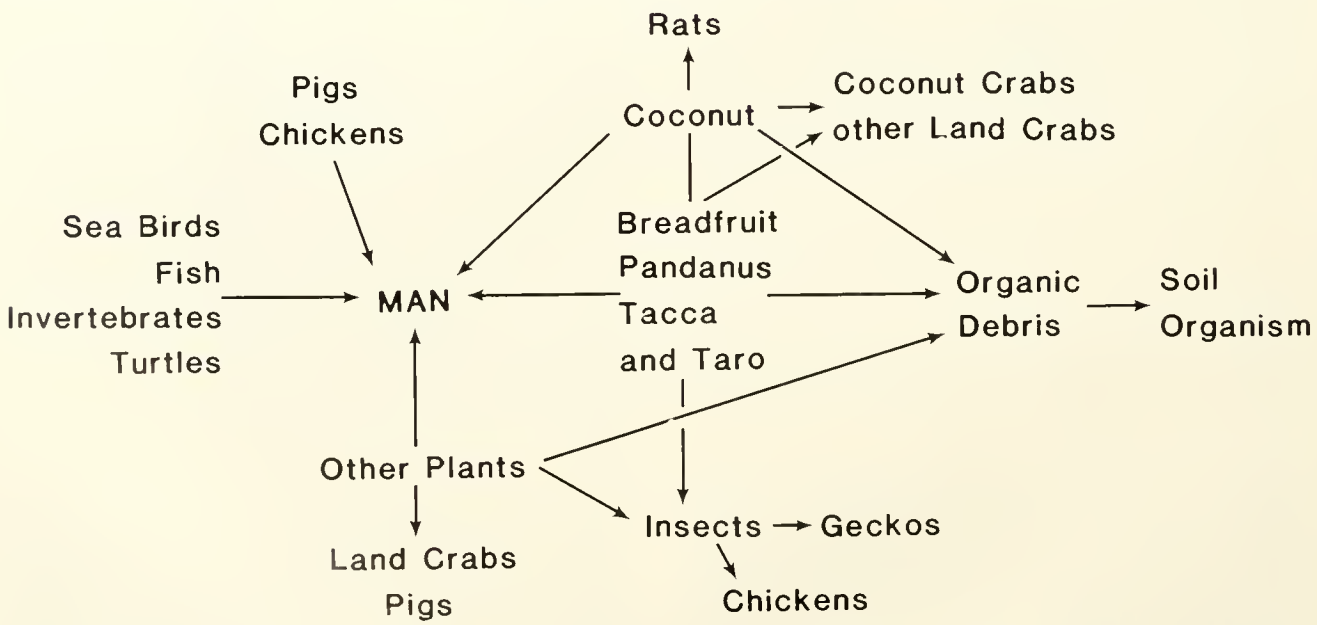

Fig. 6 Food web, energy-flow pattern for the Enewetak ecosystem showing major food pathways to man. Marine organisms are to the left and terrestrial organisms on the right side of the diagram. It has not been possible to show all pathways. For example, seabirds and their eggs are consumed by land crabs, rats, and man. Coconut crabs are eaten by man. Only plants are shown as contributing to organic debris, but waste products from animals as well as their remains also contribute to organic debris.

Needless to say, as the human population increases, the availability of natural, subsistence foods will decrease, and there will be an increased dependence on a cash economy and imported foods. At this point, the atoll ecosystem, with man as an integral part, has exceeded its carrying capacity, and further degradation of the ecosystem will occur unless the deficit is balanced with imported materials.

In this regard, the observations of Domnick and Seelye (1967) on Majuro Atoll in 1967 are extremely interesting. Their tentative conclusion, based on an admittedly small sample of nine families over a period of 30 days, is that even the highest income families adhere to a subsistence diet in preference to commercial foods. They believe this is largely due to the cost of canned foods. When commercial foods are inexpensive, they are used extensively. For example, rice "is almost essential at every Marshallese meal." Tea is preferred to coffee because it is less expensive. Large amounts of sugar are consumed. Copra is the single most important source of cash.

Clearly, the present human population of over a thousand persons clustered on the three large southeastern islands of Enewetak, Medren, and Japtan far exceeds any historical population of the atoll and no doubt far exceeds the natural carrying capacity of the atoll. In fact, the present population is almost entirely dependent on subsidies of food and material goods. In my judgment, it is doubtful that the present population could ever be self-sustaining, even with cash from copra, an expanded fishing program, handicrafts, and perhaps even tourism.

Disturbance by Man

The terrestrial environment has undergone a series of increasingly severe man-made disturbances. These are summarized in Table 1. Probably significant environmental change began with the planting of coconut plantations for copra production under the supervision of the German colonial government, 1885 to 1914. Although there was no German administrator resident on the atoll, copra freighters entered by the deep east channel and anchored in the lee of Japtan Island. Soil from north Germany, carried as ballast, was offloaded onto Japtan as copra was loaded. The extent of this operation is unknown, but Japtan Island is 1 to 2 m higher than the other islands and supports lush vegetation. Presumably soil organisms were introduced, but they have not been studied. Foreign visitors were discouraged during this time.

Following the defeat of Germany in World War I, Japan took control of the Marshall Islands under a mandate from the League of Nations, 1914 to 1944. Copra production continued, and Japanese traders resided on the atoll. In 1939 the Japanese began to construct military fortifications on Enewetak including an airstrip on Enjebi Island. Several thousand Japanese military personnel lived on the atoll. According to Hines (1962), the Japanese garrison on Enewetak numbered 2686 armed troops and about 1000 other personnel in January 1944.

Environmental perturbation must have increased dramatically during the war years culminating in the bombardment and capture of Enewetak by American forces in February 1944. Aerial bombardment coupled with naval gunfire, land-based artillery, and the effects of small arms

TABLE 1

Chronology of Man-Made Disturbances of the Terrestrial Environment of Enewetak Atoll, Marshall Islands

1. About 2000 years ago human beings settled in Micronesia (Craib, 1983), presumably including Enewetak Atoll.
2. Discovery Era, 1526 to 1885 (Buck, 1953; Emery et al., 1954; Hines, 1962; Kiste, 1974; Sharp, 1960).
   a. The first European to visit the Marshall Islands was the Spanish explorer Alvaro de Saavedra in 1529. He landed at an island, the description of which fits Enewetak, on Oct. 1, 1529. Other Spanish galleons sailed through the islands during the 16th century. There are few details and no way to know whether or not Enewetak was visited.
   b. Sir Francis Drake aboard the *Golden Hind* may have visited the Marshall Islands in 1579. Then, for the next 200 years, apparently no Europeans visited the Marshall Islands.
   c. In the 18th century, a number of famous European explorers arrived. In 1767 Samuel Wallis in HMS *Dolphin* rediscovered the northern Marshall Islands from old Spanish charts. In 1788 he was followed by Captain John Marshall for whom the islands were named. Apparently Marshall visited only the southern islands. Whether Enewetak was visited is unknown.
   d. Enewetak Atoll was rediscovered on December 13, 1794, by Captain Thomas Butler commanding the British sloop *Walpole*. He named the uncharted islands Browne's Range, and he apparently also referred to Enewetak as Walpole's Island in his journal. He did not land. Captain John Fearn aboard the *Hunter* is said to have surveyed and charted the atoll in 1798. Enewetak was often referred to as Browne or Brown Atoll even during World War II.
   e. From a scientific standpoint, the most important expedition was commanded by Otto von Kotzebue aboard the *Rurick* in 1816 to 1817. He called them the Ratak Islands and believed he had discovered them (Kotzebue, 1830). Adelbert von Chamisso, an extremely competent naturalist, was a member of the expedition. He made the first observations of the geology and

(This table continued on next page.)

TABLE 1 (cont'd)

natural history, including the first chart of the Marshall Islands. The surgeon and zoologist Frederick Eschscholtz made zoological collections. Enewetak Atoll in its extreme northwesterly position seems to have been missed; however, he visited Bikini Atoll which he named Eschscholtz Island. Kotzebue again visited the Marshall Islands for further exploration in 1824.

f. In 1841 Lt. Charles Wilkes, commanding the U. S. Exploring Expedition in the *Peacock* and the *Flying Fish*, visited the northern Marshall Islands. Charts were made of some of the atolls along with valuable observations on their natural history. For example, while chartering Rongerik Atoll, Wilkes observed no coconut or pandanus trees and saw no humans. There were other visits during the second half of the 19th century, particularly by whaling ships.

g. The first missionaries arrived in the Marshall Islands in 1857. It is not clear when their influence was first felt at Enewetak.

3. German Protectorate, 1885 to 1914.
No Europeans lived on Enewetak Atoll during this period. The German administration was on Ponape. The Germans encouraged the Enewetak people to grow coconuts for copra, which they sold to German traders. This had the effect of shifting the Enewetak society from a subsistence economy to a mixture of cash and subsistence.
4. Japanese Mandate, 1914 to 1944.
The Japanese seized Enewetak and all other German possessions in Micronesia in 1914. Subsequently, they continued to control the islands under mandate from the League of Nations. Although a Japanese trader and two assistants resided on Enewetak, the administration continued to be from Ponape. A number of Japanese scientific parties visited the Marshall Islands, but little happened until 1939 when the Japanese began to fortify Enewetak including building a landing field on Enjebi Island. There were several thousand Japanese military personnel living on Enewetak from 1941 to 1944.
5. United States Forces captured Enewetak in February 1944. Heavy aerial and naval bombardment preceded the battle which lasted several days, from February 17 to 22. The Battle of Enewetak was the last assault against a defended atoll in World War II.
6. At the end of World War II, the United States was given trusteeship of the Micronesian Islands, formerly under Japanese control, by the United Nations.
7. In December 1947, the Enewetak people were transferred to Ujilang Atoll. At this time the population was about 141 people.
8. From 1948 to 1958, the United States undertook a series of 43 nuclear tests at Enewetak. From 1958 to 1977, the atoll was used for other quasi-military purposes. This was a time of major environmental disturbance to the atoll. Buildings, testing facilities, roads, and airfields were constructed. The human population fluctuated from several dozen to several thousand during this period, depending on the testing operation.
9. In 1954 the Enewetak Marine Biological Laboratory was established. It was operated by the University of Hawaii from 1954 to 1983 with funds allocated by the Division of Biology and Medicine of the U. S. Atomic Energy Commission. The name of the laboratory subsequently was changed to the Mid-Pacific Marine Laboratory and later, to further reflect the scope of its operation, to the Mid-Pacific Research Laboratory. For a history of the laboratory and its operation, see Chapter 1 of this volume.
10. In 1972 the U. S. Atomic Energy Commission began radiological surveys of the atoll in preparation for the rehabilitation and resettlement of the Enewetak people.
11. In 1977 the United States Government began the radiological cleanup and rehabilitation of the atoll. The work was completed in 1979.
12. In April 1980, Enewetak Atoll was officially returned to the Enewetak people (see Chapter 2 of this volume for further details).

fire and flamethrowers almost denuded some of the islands—especially Enjebi, Enewetak, and Medren—of their vegetation. In the 1960s and 1970s a single tall coconut palm on Enewetak Island, which had a bend halfway up its trunk presumably due to damage sustained in 1944, was said to be the only coconut tree to survive that turbulent period. From 1944 to 1980, Enewetak was under U. S. trusteeship granted by the United Nations.

In 1947, the Enewetak people were removed to Ujilang Atoll, and the United States government began 10 years of testing of nuclear explosives on the atoll, 1948 to 1958. Again there was a major impact on the relatively fragile biota due to the construction of the test facilities and the 43 nuclear tests. Finally, in 1977 the U. S. government undertook a major cleanup of the atoll in preparation for its return to the Enewetak people (Kiste, Chapter 2, this volume).

From the standpoint of terrestrial ecology the most significant aspect of the clean-up operation was the removal of radioactive soil from many of the islands on the northeast rim of the atoll. The contaminated soil was interred with a slurry of concrete in two nuclear craters on Runit Island.

Only the five islands on the south rim of the atoll, lying west of the deep south channel, and Biken Island on the west rim were relatively unscathed by these events. On Ikuren, Mut, and Boken Islands the gradual replacement of the coconut trees, *Cocos nucifer*, planted in rows under German influence and now nearing senescense, by *Pisonia grandis* trees is especially evident.

Man-made disturbances of the Enewetak ecosystem, particularly those resulting from World War II and the subsequent nuclear testing program, probably were as devastating as any that occurred on any other Pacific island in history. What is remarkable is that with time the ecosystem has demonstrated an astonishing resilience. In a matter of 20 to 30 years the vegetation and its associated biota were capable of recovering at least to the early stages of ecological succession, and on the islands on the southwest rim of the atoll a mature *Pisonia* forest was becoming evident within that time frame.

THE FUTURE OF THE ENEWETAK ECOSYSTEM

The key to the future of the terrestrial ecosystem of Enewetak is in the hands of man. Environmental degradation brought on by overpopulation, rather than contamination by radionuclides, is now the principal threat to the Enewetak ecosystem. The people of Enewetak were not exposed to radiation. During the nuclear testing program they lived on Ujilang Atoll, albeit under conditions of hardship, and did not return to Enewetak until the cleanup of radioactive material on the atoll was completed. Although islands like Runit and a few of the severely disturbed islands on the northwest rim of the atoll will remain uninhabitable in the foreseeable future, the major islands of the atoll, especially the traditionally inhabited islands of Enjebi, Japtan, Medren, and Enewetak, should once again become attractive places for human habitation. Enewetak Atoll probably will never again be a self-sustaining island ecosystem in the sense of carrying capacity for its human population, but it can become a productive and contributing part of the Marshall Islands. It will take careful planning, strong community leadership, including birth control and family planning, and continued support from the United States government to achieve this goal.

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Chapter 12

Biology of the Rodents of Enewetak Atoll

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INTRODUCTION

Rodents at Enewetak were casually observed or occasionally specifically studied during the nuclear test program (1948 to 1958). However, the rats frequently were misidentified; no unified analysis was attempted, despite their being the only resident mammals on the test islets. When Jackson was invited to join the University of Washington's resurvey expedition in 1964, the foundation for more than a decade of studies by Bowling Green State University staff and students was established. Ten graduate students participated in these efforts, and data from their theses and dissertations are included in this discussion. The inclusion of one of these students (Temme) in the 1978 Northern Marshall Island Radiological Survey permitted collection of additional specimens and data from other atolls.

Origin and Distribution

Three rodent species are present at Enewetak. The Polynesian rat *(Rattus exulans)* came with the early Micronesian inhabitants to the atoll. The house mouse *(Mus musculus)* may have arrived with the Japanese administrators before World War II, but major infusions probably came with American activities. The roof rat *(R. rattus)* apparently arrived with American forces during or after the war. The Norway rat *(R. norvegicus)*, though present elsewhere in the Marshalls, has not been observed or trapped at Enewetak (or Bikini).

Probably the Polynesian rat occurred on most islets used by the Enewetak people for coconut culture, but the combined effects of clearing and construction and the detonation of test devices decimated many islet populations of this species. It remains on the less disturbed, more densely vegetated islets.

The roof rat has flourished on some of the heavily impacted northern islets as well as the main atoll bases (Enewetak, Medren). The survival of this species in Enjebi, within the impact zone of a nuclear detonation (Mike) as well as numerous atomic tests, is hypothesized by Jackson (1969). In an Atomic Energy Commission (AEC) experiment it was introduced to Ananij Islet, where it has flourished; other introduction attempts were made during the test program but apparently were not successful (Fig. 1).

The Polynesian rat and roof rat exist allopatrically at Enewetak. Such separation is not total on other Marshall atolls, and one Bikini islet has sympatric populations. The house mouse was found on only three islets (Enewetak, Medren, Japtan) but was in combination with roof or Polynesian rats.

Cats and dogs existed in varying numbers on islets inhabited by test or administrative personnel (Japtan, Medren, and Enewetak, during our studies). While these animals occasionally caught rodents, they did not seem to have any impact on the populations. Monitor lizards on Japtan caught some rodents, but the impact of such predation was apparently insignificant. Coconut crabs *(Birgus latro)* were scavengers rather than predators and were observed eating opened coconuts alongside Polynesian rats on Igurin. Reef herons *(Egretta sacra)* may have been predators, but we did not observe such behavior.

House Mice

Mice were found in buildings (occupied or unoccupied) on three islets (Enewetak, Medren, Japtan), and we also caught them regularly in grassland and shrub habitats on these same islets. Detailed studies of house mice were conducted on Enewetak and Medren islets (Berry and Jackson 1979; Berry et al., 1981). These two populations were genetically different, both in terms of external morphology (pelage) and allozymic variation. Mean heterozygosities (per locus) for these two islet populations were high, 11.4% and 10.9%, respectively. Such variability has been exceeded only in Hawaii (Berry et al., 1981). Selection for certain loci with age, which occurs in nontropical environments, was not observed in these populations. Berry (1979) suggested that such high genetical variability could

Fig. 1 The Polynesian rat, *Rattus exulans*, and the roof rat, *Rattus rattus*, are distributed allopatrically at Enewetak; a, The Polynesian rat is found in more densely vegetated habitats and is particularly abundant on the larger islands where coconut trees were planted for copra production. (Photo by William B. Jackson of Japtan Island in 1971); b, The roof rat is found in more disturbed open habitats, particularly the northern islands of the atoll. (Photo by William B. Jackson of Enjebi Island, looking to the southeast, taken in 1967). The remains of the former Japanese airstrip is visible in the foreground, and the nuclear test building, now demolished, is seen in the middle distance.

be an adaptation to reduce intraspecific competition under conditions where a variety of foods is readily available.

The mice were smaller in body size than mainland forms (9 g vs. 15+ g); this was hypothesized by Berry and Jackson (1979) to be an adaptation to the constant high temperatures in a situation where predators are generally absent. Both populations were considered to be western (rather than Asiatic) in origin, supporting their hypothesized introduction after World War II.

The high density Polynesian rat population on Japtan islet interfered with specific trapping efforts there, and no comparable studies were possible. We did occasionally observe different pelage forms there, suggestive of animals having escaped from laboratory colonies maintained during the test program on this islet and interbreeding with the local population.

Two breeding peaks (January through February and July through August) were observed. Average litter size was 4.0.

Habitat Selection

The Polynesian rat is a ground-dwelling rat, although it has extensive arboreal highways, well odor-marked, through the low vegetation. Frequently palm fronds were used, which we confirmed with direct field observations under red-light conditions and later in a simulated environment in our home laboratory using fronds brought back from Enewetak. Nests were rarely found but were considered to be under or among surface debris (e.g., piles of coconuts) or in shallow burrows. We never observed their feeding in the crowns of coconut trees, even where islet distribution of rats was allopatric. This species was trapped on the trunks of coconut trees and was found feeding on freshly damaged small nuts on Japtan.

This rat was found on the more densely vegetated islets but was absent from some of the smaller and/or more remote islets, especially on the western side of the atoll. We conclude, on the basis of conversations with Enewetak elders, that before the atomic tests, these rats were present only on those islets that had been regularly used in the past for coconut harvesting.

On islets such as Enjebi and Runit as well as Medren and Enewetak, which initially were infested by Polynesian rats (based on early observations and records), clearing and construction activities and test device detonation (in the case of Enjebi and perhaps Runit) eliminated them. These islets are now occupied by only the roof rat. Whether interspecific competition was a factor in these local extirpations of the Polynesian rat is not known. Accidental transport of rats by man (initially by the Micronesians in their canoes, later by AEC and military personnel in supply craft) is considered the primary mode of spreading rats around the atoll. Both tidal flow patterns and abundance of predatory fish reduce the likelihood of direct water transport.

The roof rat infested coconut crowns when these trees were present. Although they readily climbed available vegetation, they traveled easily on the ground surface. They used surface debris or shallow burrows for nest sites; they also dug around bunker foundations. This species prospered on the more disturbed islets, those having less cover, but was absent from more remote islets having minimal human activity during the atomic test program.

The Polynesian rat and the roof rat readily invade structures, and almost all storage and inhabited buildings were infested. The facility at Lojwa during the cleanup operations had a particularly difficult time with invading Polynesian rats. The initial population density was high, and vegetation removal forced the concentration of surviving rats in a perimeter strip. As soon as buildings were erected, rats took up residence.

Popuiation Density and Home Range

Live-trapping, mark-and-release studies were undertaken for roof rats on Runit and Polynesian rats on Japtan. Roof rat population density in this open, grass-sedge-shrub environment was about 20 animals 11,000 m^{-2} or about one animal 550 m^{-2} (Jackson, 1967). This density may have been exceeded in subsequent years on Japtan with diminished human disturbance; frequently, we caught two rats in the same snap trap.

In these environments, the home range (as measured by standard diameter) for roof rats was 67 m for females and 100 m for males. For Polynesian rats, it was 50 m (both sexes).

Food Habits

Rats, even though at the apex of the terrestrial food pyramid, are largely vegetarians in this environment. In a study of food habits, Fall et al. (1971) found arthropod (insects, centipedes) remains somewhat more frequently in roof rat than Polynesian rat stomachs (33% vs. 10%). Additional studies at Enewetak and on the Northern Marshall Islands Radiological Survey reaffirmed these patterns; however, the volume of animal matter was small (<2%) (Temme, 1982). Seasonal fruits and seeds, as well as vegetative plant structures, were recognized in the stomach contents.

Roof rats occasionally were seen at night foraging on the beach and even out onto the exposed reef flat. Fish (trapped in tidal pools) may well have been caught or scavenged, though we did not observe this.

In a simulated predation situation with roof rats confined to beach enclosures, we did, with starlight scopes and under direct moonlight, observe rats enter ghost crab (*Ocypode* sp.) burrows, pull the crab out, dismember, and eventually eat the crab. Often the eye stalks were the initial target of the rat.

When we captured rats in the vicinity of ground-nesting tern colonies, we occasionally found bird remains in the stomachs. We were unable to determine if this resulted from predation or scavenging. In one instance, we found opened eggs in a portion of a sooty tern colony and

suspected Polynesian rat depredations. However, this was an isolated, not a repeated, observation.

Reproductive Patterns

Necropsy data, assembled over 14 years and available from all months except May and December, provide a composite picture of breeding patterns. For Polynesian rats, a bimodal increase in prevalence of pregnancy is significantly correlated ($r^2 = 0.82$) with spring and fall rainy seasons. The fall period is longer, and the prevalence of pregnancy reaches nearly 0.25 in October (Temme, 1981). We hypothesize that the increased food supply (and perhaps cover) associated with increased precipitation is the basis for greater reproductive activity (Fig. 2).

Despite the general data correlations, some individual islet variations were observed. If coconut trees were present, pregnant rats were more likely to be found. However, sufficient data were not collected to delineate the extent of these intra-atoll variations.

On the basis of embryo counts, average litter size for Polynesian rats was determined to be 3.3 (Table 1). About a third (36%) of the pregnant females were primiparous. These reproductive data are similar to those obtained elsewhere in the tropics for this species.

Most males (84%) had scrotal testes, and few young males were caught early in the breeding seasons. Accessory organs (e.g., seminal vesicles) regressed in size during the nonbreeding January period and recrudesced in March. However, the variations in seminal vesicle length and prevalence of pregnancy were only weakly correlated ($r = 0.42$). Some effects of population density and stress are suspected (Temme, 1981).

Data from roof rat populations followed very similar patterns, showing the same summer and fall reproductive peak (Table 1); however, litter sizes were larger, averaging 4.2 young.

Behavior and Population Regulation

An atoll provides an unusual opportunity to study natural rat populations because of the number of similar islets in isolated proximity. Population densities vary from islet to islet but are typically higher than those on the

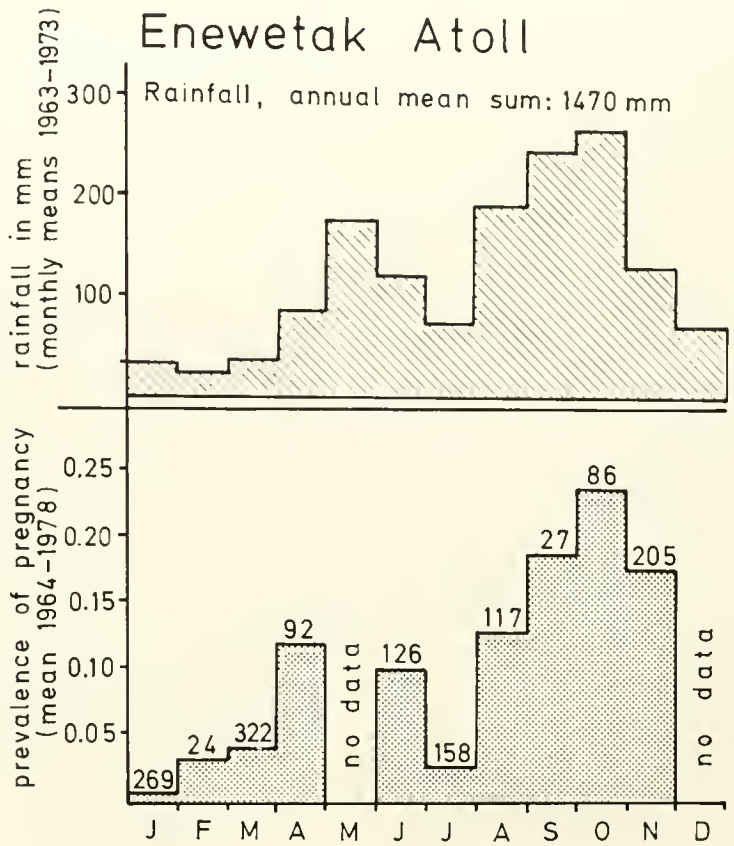

Fig. 2 Relationship between monthly mean rainfall and prevalence of pregnancy of Polynesian rats (means 1964 to 1978). Sample sizes (tops of bars) are based on mature females (perforate vaginal orifice) (Temme, 1979).

TABLE 1

Summary of Female Rat Reproductive Data from Northern Marshall Islands

	Winter (Dec.–Feb.)	Spring (Mar.–May)	Summer (Jun.–Aug.)	Fall (Sept.–Nov.)	Totals
Polynesian rats*					
No. with vaginal orifices perforated	293.0	414.0	437.0	318.0	1462.0
Percent pregnant	1.0	7.7	15.6	17.6	10.9
Embryos/female	3.3	3.2	3.2	3.4	3.3
Roof rats					
No. with vaginal orifices perforated	149.0	405.0	323.0	180.0	1057.0
Percent pregnant	4.0	6.2	14.5	21.7	10.5
Embryos/female	3.5	4.4	4.5	3.7	4.2

*From Temme (1981).

mainland; dispersal is nearly absent. In this context, Krebs, Keller, and Tamarin (1969) have shown that blocking dispersal leads to unusually high densities in some rodent species.

Adrenal gland weight has been widely used to assess the role of agonistic behavior in inducing a physiological stress response. Laboratory and field studies have demonstrated a positive correlation between adrenal gland weight and both population density and loss of fights (reviewed by Christian, 1978). Other work has demonstrated inhibitory effects of crowding and aggression on reproductive function and disease-defense mechanisms. In this Enewetak study (1977 to 1978), the relationships between population density, adrenal size, wounding, and parasite load were examined.

Trapping

Conventional Victor kill traps, baited with fresh coconut, were set at approximately 7-m intervals before sunset, emptied and rebaited several times during the night, and pulled at midnight or the next morning. Because of the variability in trapping effort, results are expressed in rats caught per trap hour rather than per trap night.

Necropsy

Routine body measurements and reproductive data of scrotal males and sexually mature, nonpregnant females were noted; adrenals were preserved in 10% buffered formalin and later cleaned and weighed wet. The ratio of the combined adrenal weights to the head and body length was used in all subsequent calculations. Small intestines were removed and also fixed in buffered formalin; later they were opened and tapeworms counted. After clipping hair from the posterior one-third of the back, remaining hair was removed with a depilatory; fresh wounds were counted.

Population Density and Adrenal Weight

On five Polynesian rat islets, with densities ranging from 0.06 to 0.58 rats caught per trap hour, no consistent relationship between population density and adrenal weight was apparent for either sex.

For five roof rat islets, with densities ranging from 0.006 to 0.062 rats per trap hour, correlation analysis revealed a significant, positive relationship between density and adrenal weight in both sexes for this species (Fig. 3). Enewetak Islet had a low population density, because of a control program, and the lowest adrenal weights. Medren, with large numbers of abandoned buildings, supported the densest population and the heaviest adrenal weights. Other islets were intermediate. Population densities on Enjebi increased from 0.029 in 1977 to 0.045 in 1978, probably because the island was chained between samples, and the cut vegetation was placed in piles as part of a cleanup program, thus concentrating the survivors. Adrenal weight/body length ratios correspondingly increased from 0.28 (males) and 0.27 (females) to 0.40 (males) and 0.44 (females) (Table 2).

Population Density and Wounding

The mean number of back wounds per rat (species combined) increased as population density increased (Fig. 4). Males generally had more wounds than females, particularly on the densely populated Polynesian rat islets of Bijire and Aomon. On low density, mainly roof rat islets, sex differences were not great.

Wounding and Adrenal Weight

Polynesian rats with fewer than two wounds had significantly lower adrenal weights than did those with two or more wounds (t-test, $P < .001$, both sexes; Table 3). For the less frequently wounded roof rats, both males and females with no wounds had significantly lighter adrenals than did those with wounds (t-test, $P < .025$).

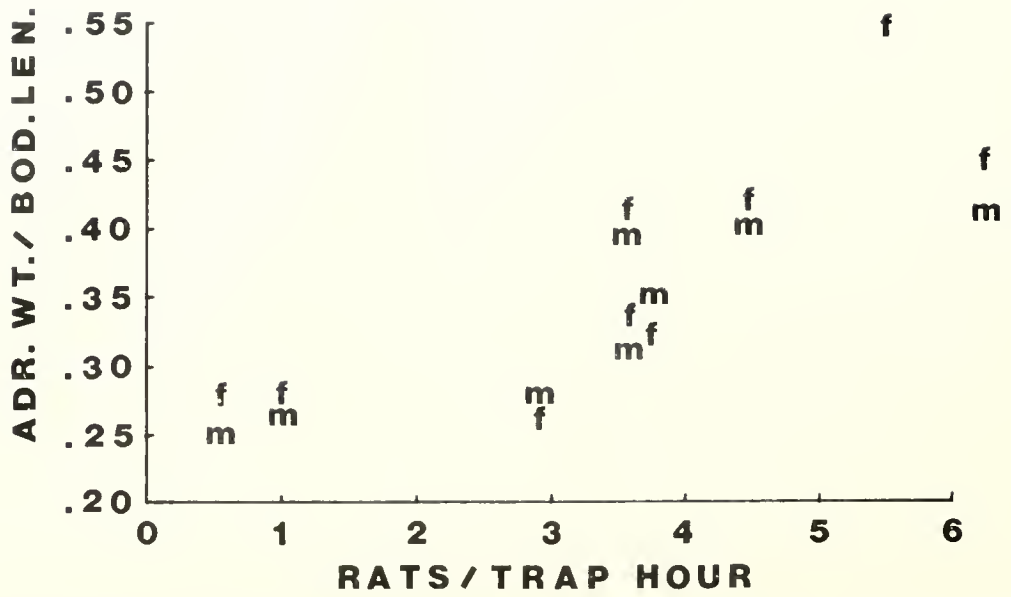

Fig. 3 Rats per trap hour (× 100) and adrenal weight/body length ratios for roof rats plotted separately by islet (1977 and 1978); f = females, m = males.

TABLE 2
Summary of Population Density Estimates and Adrenal Gland Weights for Roof Rats at Enewetak Atoll

Islet	Population*	Adrenal wt./ body length	
		Males	Females
	1977		
Enewetak	0.58	0.250	0.278
Enjebi	2.92	0.275	0.268
Ananij	3.55	0.388	0.405
Runit	3.67	0.300	0.330
Medren	6.23	0.387	0.438
	1978		
Enewetak	1.01	0.269	0.276
Ananij	3.75	0.349	0.298
Enjebi	4.49	0.401	0.471
Medren	5.52		0.532

*Rats/trap hour × 100.

Parasites and Adrenal Weight

Two parasites were examined in the rats. The most common was a stomach worm of the genus *Protospiura*, which was present in both species. The incidence or burden of this parasite was not related to adrenal weight. The other parasite was an intestinal tapeworm, *Hymenolepis diminuta*, which was common only on Aomon. Rats of both sexes which had tapeworms had heavier adrenals than did those without tapeworms (t-test, $P < .05$; Table 4).

Discussion

The results generally support the idea that as population density increases so does the incidence of fighting, an observation made many times in simulated free-living laboratory colonies and in field observations under red lights and with starlight scope. As a result of fighting, certain individuals—the losers of these fights—undergo a stress response leading to increased production of glucocorticoid hormones and hypertrophy of the cortex of the adrenal gland. Although these hormones prepare the body for fight or flight, they also are associated with a decrease in reproductive hormones and the suppression of the body's defense mechanisms. We have not examined the relationship between adrenal hormones and reproduction; but rats that were under stress were more likely to have tapeworms, suggesting the predicted inhibition of defense mechanisms against disease. The failure to find an effect with the stomach nematode may have been because this parasite, while residing in the stomach, does not attach to the host or otherwise stimulate an inflammatory or immune response.

The failure of the Polynesian rat to show a consistent adrenal response with islet population density is difficult to explain. However, this species typically lives at much higher densities and seems more tolerant of crowding than the roof rat. Although fighting is common among Polynesian rats, as evidenced by simulated free-living laboratory

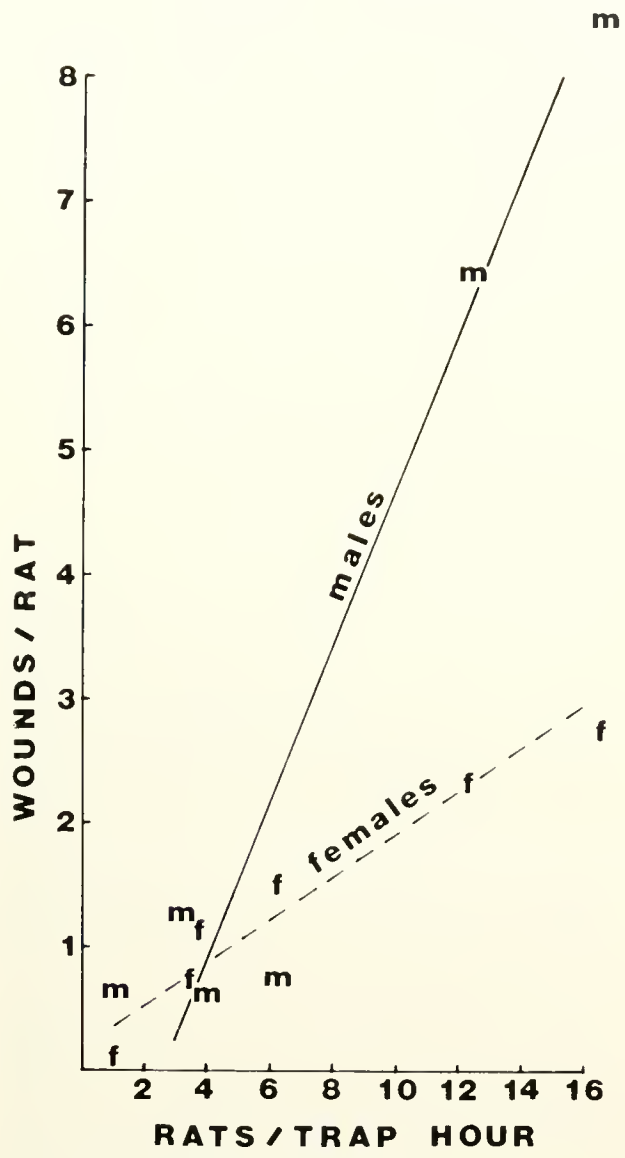

Fig. 4 Rats per trap hour (× 100) and mean wounds per rat (roof and Polynesian rats combined) for each islet (1978); f = female, m = males.

colonies and direct field observations and the incidence of wounding, possibly these fights are not as severe or stressful as with the roof rats.

Although it is likely that food sets the upper limit to density on these islets, with the absence of dispersal and predation as regulatory mechanisms, it also seems likely that physiological changes associated with crowding act to adjust birth and death rates to keep numbers below the point where starvation occurs.

Stomach Parasite Loads

The stomach nematode *(Protospiura muricola)* was not uniform in distribution. Although present in all Polynesian rat populations studied by F. C. Rabalais at Enewetak (average prevalence = 0.32; Table 5), it was not found at Bikini Atoll and Mejit Island in the Northern Marshalls survey (Temme, 1979). The parasite load was small in both studies, about two parasites per rat.

In contrast, this parasite was not found in all roof rat populations at Enewetak Atoll; Ananij and Enewetak rats lacked the worm (Table 5). However, the average prevalence on the other islets was 0.56. The average parasite load was 10 times that in the Polynesian rat.

A second stomach nematode *(Gongylonema neoplasticum)* was found by Temme (1979). Because it is imbedded in the mucosal lining, it is not often recorded. It was found in nearly half the rats in all populations studied (Table 5). However, the parasite load averaged 1.7 worms per rat. About half the rats were infested with both nematodes.

In the case of both host species, the larger animals tended to have more parasites. Some roof rats had in excess of 75 *Protospiura*. Even so, these parasites did not appear to be a serious stress factor.

TABLE 3

Summary of Enewetak Atoll (All Islets, 1978) Wounding and Adrenal Weight Data for Roof and Polynesian Rats

No. of wounds	No. of animals	Sex	Adrenal wt./ body length	P(t-test)
		Rottus exulans		
<2	39	F	0.142	
	44	M	0.103	
2 or more	55	F	0.192	<0.001
	45	M	0.144	<0.001
		Rottus rattus		
0	47	F	0.341	
	28	M	0.323	
1 or more	20	F	0.414	<0.025
	26	M	0.411	<0.005

TABLE 4

Summary of Tapeworm Infestations in Polynesian Rat Relative to Adrenal Weight, Aomen Islet

Sex	No. of rats	Tape-worms	Adrenal wt./ body length	P(t-test)
Male	9	No	0.111	<0.05
	9	Yes	0.142	
Female	4	No	0.100	<0.05
	9	Yes	0.138	

*Aomen islet, Enewetak Atoll.

TABLE 5

Summary of Stomach Nematode Distributions Relative to Host Species, Islet, and Atoll

Species and parasite	Islet	No. rats	No. infected	% infected
	Enewetak Atoll			
R. rattus	Enewetak	14	0	
(Protospiura	Runit	92	19	20.7
muricola)	Enjebi	56	47	83.9
	Ananij	45	0	
	Medren	58	49	84.5
	Totals	266	115	43.2
Totals (infected islets)		206	115	55.8
R. exulans	Japtan	105	30	28.6
(Protospiura	Lojwa	20	11	55.0
muricola)	Bijire	34	17	50.0
	Aomon	44	12	27.2
	Ikuren	59	12	20.3
	Totals	262	84	32.1
	Northern Marshall Atolls			
R. exulans (Protospiura muricola)		602	141	23.4
(Gongylonema neoplasticum)		602	208	46.5

*Temme, 1979.

TABLE 6

Average ^{137}Cs Levels (pCi g^{-1} Dry Weight) of Soil Samples and Plant and Animal Tissues Collected on Runit Islet (1967)*

	Distance from Cactus Crater, m				
	0	200	1030	1710	2460
Surface soil	34.4	10.8	2.4	3.7	0.5
Scaevola fruit	437.5	56.1	7.5	20.4	1.7
Tournefortia leaves	2174.0	76.8	49.0	30.4	2.0
Roof rat liver	2261.0	276.0	38.8	11.0	3.5
Roof rat kidney	5134.0	722.0	95.6	38.0	4.7

*Numbers of samples vary. Data from Bastian and Jackson, 1975.

Responses to Testing Program

During the Atomic Energy Commission's testing program, detailed or systematic studies on rodents were not conducted, although several individuals made brief observations and even transplanted rats from islet to islet. In some cases, it was possible to reconstruct the experiments and even correctly identify the rodent species involved. However, it was not until the 1964 Resurvey Program, directed by the University of Washington, that continuing studies of the rodent populations were initiated.

At that time, roof rats inhabited the larger, highly disturbed islets; Polynesian rats inhabited the less disturbed islets. Our radionuclide investigations focused on the roof rat populations on Enjebi and Runit, although we studied populations, including Polynesian rats, on other islets.

On Runit we examined roof rats at varying distances from Cactus crater at the north end of the islet (Bastian and Jackson, 1975). The rats concentrated the radionuclides they obtained from plants in their diet. At the crater, levels of ^{137}Cs ranged up to about 2000 pCi g^{-1} (dry weight) in plant tissues; in rat tissues, to 5000 pCi g^{-1} (Table 6). At the south end of the islet (where no testing was done) radioisotope levels were close to background. We felt, on the basis of these data, that rats would make excellent radiation monitors.

Further efforts to demonstrate the potential monitoring role of rats led to the use of thermoluminescent dosimeters (TLD), which were implanted under the nape skin of rats that were released and then recaptured 5 months later (1977 to 1978). Of the 185 implants made, 39 were recovered, even though cleanup operations were under way, which greatly interfered with the initial trapping and recapture operations. Rats of both species on six islets were involved. Exposures of 3 to 7 mR d^{-1} were recorded from rats on Runit and about 1 mR d^{-1} on Enjebi are contrasted to zero readings in Igurin and Ananij rats. These radiation levels detected by the rats' dosimeters appear to correlate closely with the measurements obtained during the cleanup operations (Table 7).

The aborted PACE program (1972) had a principal impact on Bijire with the removal and windrowing of plant debris. The Polynesian rats used this increased cover, and the sooty terns shifted their breeding colony to some of the cleared habitat. From examination of stomachs, we know that rats were preying or scavenging on the terns. Numbers of Polynesian rats on the three-islet chain (Aomon–Bijire–Lojwa) continued to be high during and following this period.

When the final cleanup program was organized, Lojwa was set up as a base facility (1977), and most of the land area was scraped clean. Polynesian rats were pushed into the fringe of remaining vegetation. As soon as living quarters were constructed, rat infestations became chronic problems.

Garbage was disposed of in a pit across the bridge to Bijire. Although periodic covering occurred, rats abounded. We observed rats moving from distances of several hundred meters to the dump, but no detailed marking and movement studies were possible.

The cleanup on Enjebi resulted in chaining and windrowing much of the vegetation and subsequent removal of contaminated soil and debris from many areas. The roof rats, perhaps reduced in total numbers, were concentrated

TABLE 7

Summary of Ambient and Rat-Implanted Dosimeter Exposure Results, Enewetak Atoll, November 1977 to April 1978*

Islet	No.	Ambient dosimeters, exposure (mR day^{-1}) Mean	Range	Species	No.	Implanted dosimeters, exposure (mR day^{-1}) Mean	Range
Enjebi	15	0.63	0.26 to 1.29	*R. rattus*	7	0.89	0.41 to 1.78
Runit	5	4.12	2.94 to 6.51		3	4.56	3.29 to 6.86
Ananij	9	0			9	0	
Bijiri	8	†	0.00 to 0.20	*R. exulans*	11	0.08	0.00 to 0.18
Aomon	5	0.27	0.12 to 0.43		6	0.13	0.00 to 0.20
Igurin	5	0			4	0	

*Dosimeters supplied and analyses provided by I. Aoki, Radiological and Environmental Sciences Laboratory, Idaho Operations Office, DOE. Calculated results in millirem (mR) were derived for total exposure period.

†Too low to calculate.

in these vegetation piles. Burning, however, was incomplete; resprouting of shrubs occurred rather quickly. The rats increased in numbers and began to spread.

The bulldozing of transects for radiation measurements on other islets probably had limited impact on the rats. The brush piles provided increased harborage; certainly, the carrying capacity of these islet habitats for rats was not decreased.

In our earlier studies, we had found no abnormalities in rats that we could associate with elevated radiation levels. The rats were not larger, nor did we observe a greater prevalence of tumors or resorbed embryos. Color phases were not associated with radiation patterns. The melanistic roof rats on Runit are better explained through genetic drift in an isolated population. In recent studies, however, Temme (1981, 1986; Temme and Jackson, 1978) found a positive relationship between background radiation levels and frequency of palatal ridge deviations in the roof of the mouth (Figs. 5 and 6). For example, the incidence of abnormal palatal ridges was 0.44 in Polynesian rats from Lujor Islet, which had the highest test contamination of islets still harboring this species. On Japtan, with no direct testing contamination, the incidence was 0.06. Other populations were intermediate, but similar relationships were not evident in roof rat comparisons.

However, when mean measures of divergence for palate ridge variation are compared, values between Enewetak and Bikini Atolls and between Enewetak and other atolls are much larger than statistics comparing the north end of Enewetak Atoll (greatest radiation exposure) with the southerly islets (least exposure) (0.75 to 2.0 vs. 0.20 to 0.35) (Figs. 7 and 8). Thus these palate variant patterns also may be influenced by geographic isolation—the greater the geographic separation, the larger the divergence statistic (Temme, 1981). As far as could be determined, these slightly altered palatal ridge structures cause the rat no difficulty; we do not know if a mutation is involved.

Plasma transferrins were examined by Malecha and Tamarin (1969) from roof rats collected on Runit, Enjebi, and Medren. Five alleles were found, compared to only

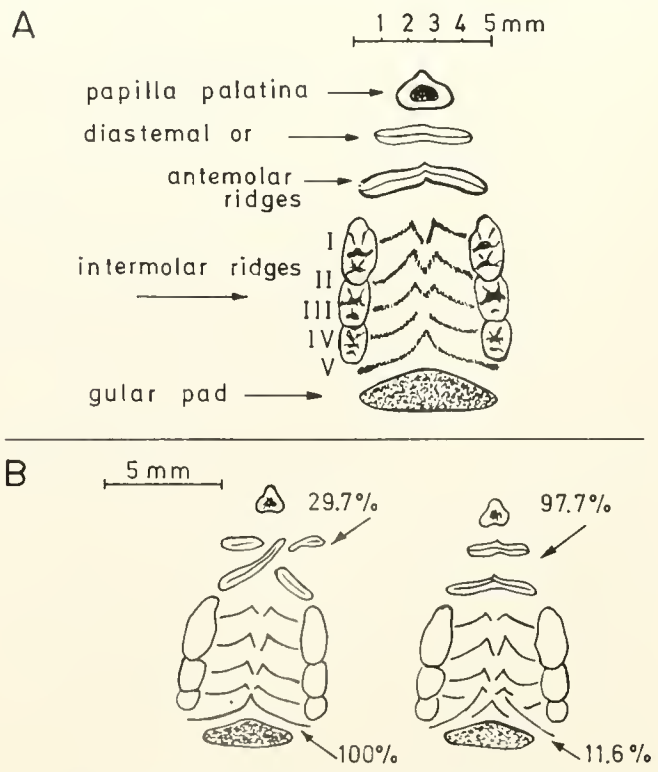

Fig. 5 a, Nomenclature of palatal ridges in typical Polynesian rat; b, Incidence of diastemal ridge deformation in rats on Lowja (Enewetak Atoll), which had intermediate levels of background radiation, was 0.30. On Japtan (outside the contaminated area) the incidence was 0.02. A new aberration, involving intermolar ridges and found in 12% of the specimens, was unique to Japtan (Temme and Jackson, 1978).

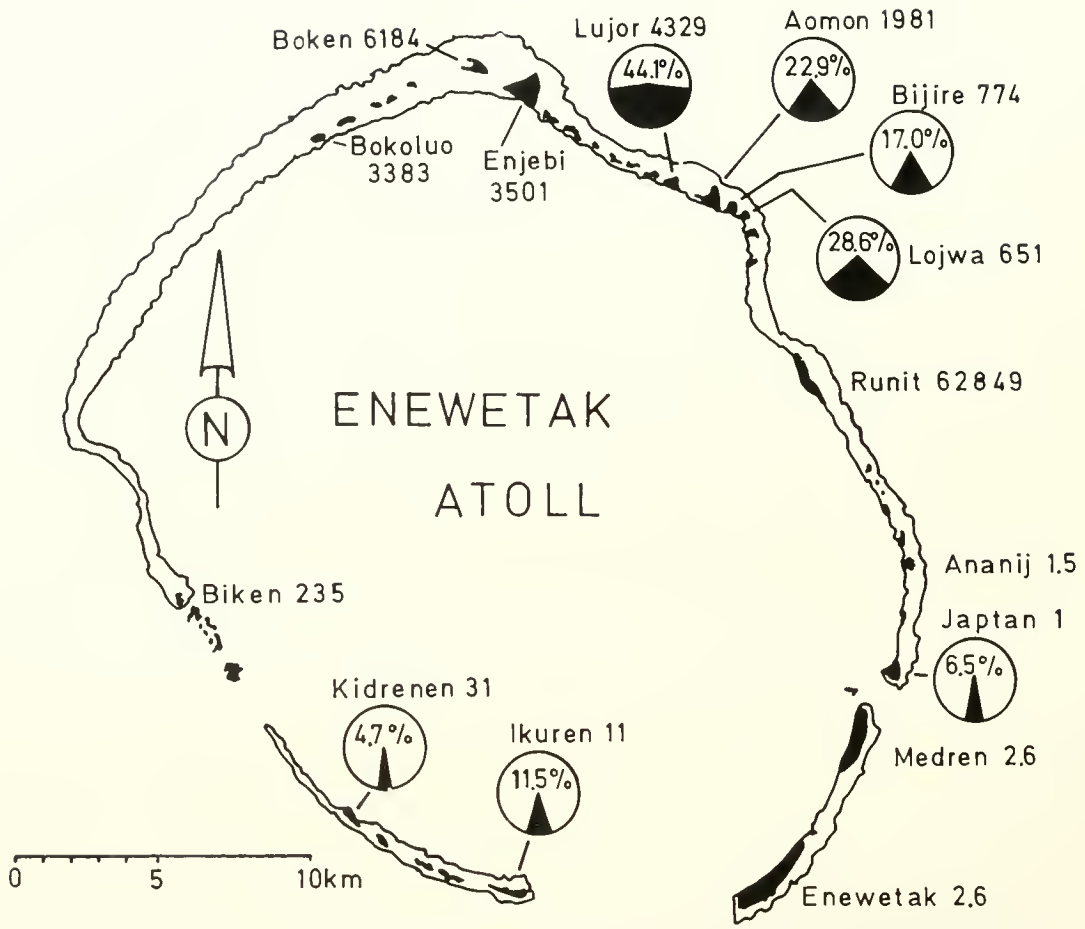

Fig. 6 The sections in the circles represent the percentage of abnormal antemolar palatal ridge pattern in the Polynesian rat populations. The four islets with the highest percentages are centered between islets with highest contamination data. These values given for several of the larger islets are average fallout contamination levels in R/hr, corrected to H + 1 hr past detonation of the atomic testing devices (Temme, 1981).

three in Hawaii. They suggested that the greater variation in the Enewetak rats might be due to the nuclear detonations.

In 1980 blood samples were taken from roof rats on Medren (N=16), Enjebi (N=17), Runit (N=35) for analysis of protein variation. Of 29 loci checked by electrophoresis, 13 were polymorphic.

Heterozygosity (the percent of all loci per individual that were heterozygous) was lowest on Medren (16.4), intermediate on Enjebi (19.7), and highest on Runit (21.1). The percentage of loci that were polymorphic also increased in the same order, from 38% to 41% to 45%. These findings raise the possibility that increased radiation also may have increased selection for heterozygotes or may have increased mutation rates on Enjebi and Runit.

Nei's (1972) genetic distance among the three islands varies from 0.95 to 0.96. Comparable data for isolated house mouse populations showed higher values, from 0.98 to 0.99 (Nei, 1972), suggesting greater isolation among the rats at Enewetak.

SUMMARY

Roof rats and Polynesian rats, introduced to the atoll by 20th century commerce and the Micronesians, respectively, were present allopatrically on the larger islets. Of necessity, they were largely vegetarians. Reproductive cycles were keyed to rainfall patterns. High density populations had high stress indices, including high parasite loads.

The rats, at the top of the terrestrial food pyramid, constituted a bioenvironmental monitor that was rarely utilized during the several test programs. Bioconcentration of radioisotopes, especially ^{137}Cs and ^{60}Co, occurred; rats implanted with dosimeters were determined to function as environmental radiation monitors. We hypothesized that roof rats on Enjebi survived the nearby nuclear detonation.

Analysis of plasma transferrins indicated greater heterozygosity in the northern atoll rat populations. The incidence of oral palatal ridge deformations also was positively correlated with environmental radiation levels, but other gross indications of radiation effect were not found.

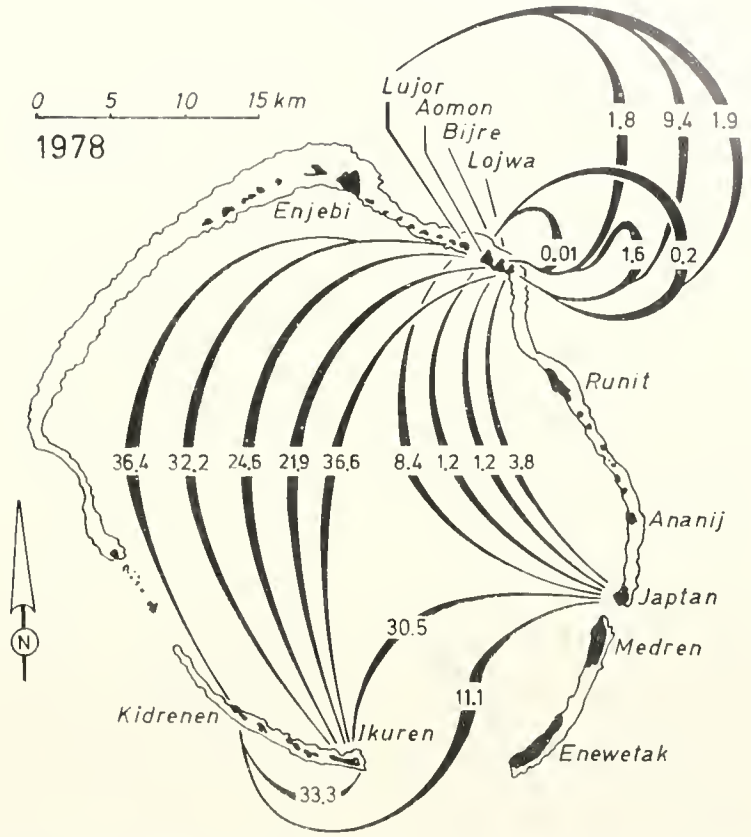

Fig. 7 "Mean measure of divergence" (× 100) for intermolar palatal ridge variations in Polynesian rats between islets at Enewetak Atoll (Temme, 1981).

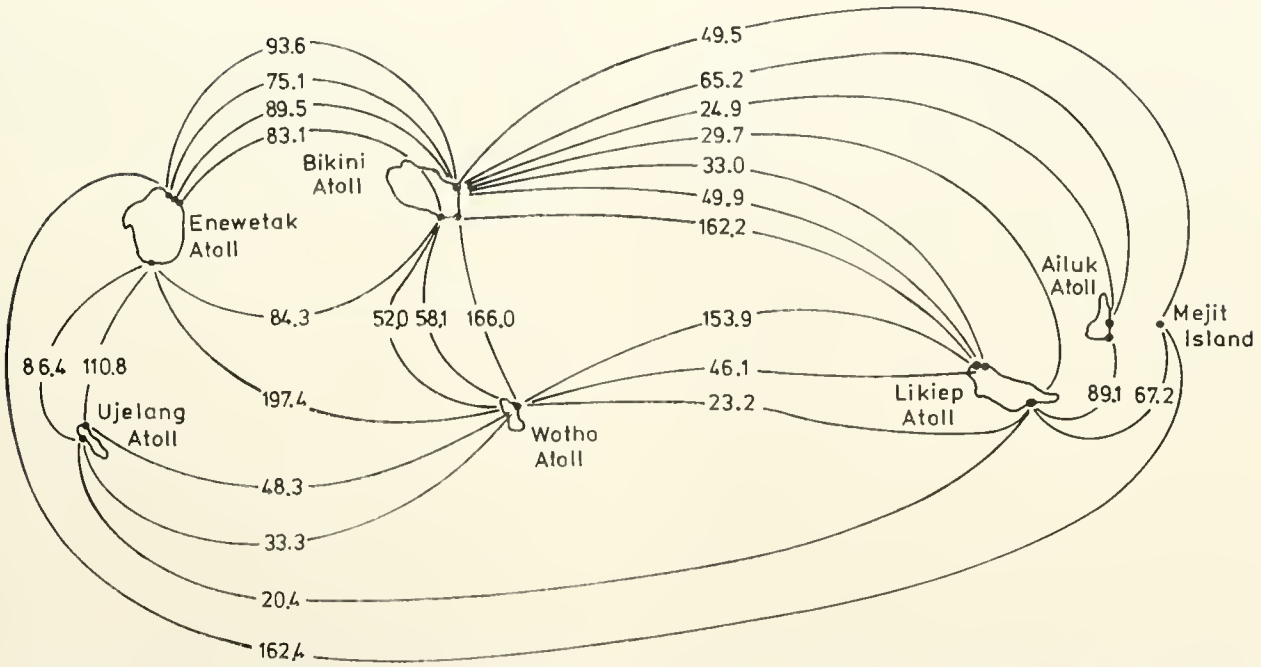

Fig. 8 "Mean measure of divergence" (× 100) for intermolar palatal ridge variations in Polynesian rats between islets of several atolls in the northern Marshall Islands (Temme, 1981).

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Initial encouragement and involvement were provided by Lauren Donaldson and other personnel of the Laboratory of Radiation Biology, University of Washington. The laboratory analyzed many of our soil, plant, and animal samples for radionuclides. Subsequent support was provided by direct AEC contract [AT (11-1)-1485], MPML (later Mid-Pacific Research Laboratory), various ERDA contractors for additional soil and animal tissue gamma counts as well as other atoll support services, and the Bowling Green State University (BGSU) Faculty Research Committee. The most recent field studies were possible because of the inclusion of Manfred Temme in the DOE Radiological Survey of the Northern Marshall Islands (1978).

Many individuals have participated in these studies. F. C. Rabalais (BGSU) contributed parasitological studies. R. J. Berry (University College, London) with assistance from the Royal Society of London conducted the house mouse studies. W. Z. Lidicker and R. D. Sage (University of California, Berkeley) carried out the mouse tissue analyses. The dosimeters implanted in the rats were prepared and interpreted by I. Aoki, DOE Radiological and Environmental Sciences Laboratory, Idaho Falls. Roger Ray and others of the DOE Las Vegas office were especially helpful in obtaining data and information. William Robison, Lawrence Livermore National Laboratory, also provided information. Additional BGSU graduate students participating in the field studies included Michael Carpenter, Tom Denbow, Michael Fall, Gail Haigh, Dale Kaukeinen, Robert Lane, Willard McCartney, and David Rintamaa.

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Chapter 13

Avifauna of Enewetak Atoll

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INTRODUCTION

Birds constitute an important element of the Enewetak fauna. They form a significant portion of the biomass of larger land animals, and they also are important foragers of the surrounding ocean, particularly of the shallow reef areas. The isolation of Enewetak—200 km from the nearest other land—dictates that the birds that have arrived there have had to be strong fliers; this is especially true for migrant species.

At least 41 species of birds have been recorded at Enewetak Atoll. Amerson (1969, and included in the EIS of 1974) listed 32 species; Johnson and Kienholz (1975) added three; Temme (1979) and Hailman (1979) added six more. A checklist is included as Table 1. These birds are described and illustrated by King (1967). Earlier papers dealing with the avifauna of Enewetak were those of Gleize and Genelly (1945), Woodbury (1962), Pearson and Knudsen (1967), and Carpenter et al. (1968).

No endemic species and no passerine species inhabit the low islets of Enewetak. The islets presumably are too low, too small, and too remote from major land masses to have been colonized by birds that could have evolved into endemic forms (Berger, 1979). Many of the native seabirds are species that have a vast range in the Pacific region, and many of them spend only the breeding season on land. Of interest is the migration of the long-tailed cuckoo *(Eudynamis taitensis)* from New Zealand to the winter range on Enewetak and other islands from the Bismarck Archipelago eastward to the Marquesas Islands.

The bird fauna of Enewetak, however, is not well-known, primarily because few observers have been able to spend extensive periods of time on the various islets. Any significant effort over a period of time would certainly add other species to the list. For example, David Anderson (unpublished), a former Peace Corps volunteer residing on Ujelang Atoll, recorded 36 species of birds from that atoll between June 1975 and February 1977; a number of these species have not yet been recorded at Enewetak.

At least 12 species are known to breed on the atoll, and at least four others are thought to nest there. Many other birds probably include Enewetak within their range. Owen (1977), King (1967), and Baker (1951) list a number of species known from the Marshall Islands and other adjacent areas that have not yet been recorded at Enewetak. The Marshallese names for the birds of Enewetak have been listed by Goo and Banner (1963).

The importance of predators other than man on birds at Enewetak is not well-known. Amerson (1969) suggested that both the coconut crab *(Birgus latro)* and *Coenobita rugosa* eat eggs and young birds. Reese (personal communication) observed a coconut crab catch a white tern by the wing and drag it into the crab's burrow under coconut debris at the base of a coconut tree. The tern apparently had been frightened from its perch by Reese's night survey team. Certainly, land crabs are scavengers and feed on bird carcasses when they are available.

On Igurin Island, however, Helfman (1973) did not see coconut crabs feeding on either birds' eggs or young birds. He noted that coconut husk and meat, plus a variety of other items, were eaten. Igurin has large numbers of birds, and if they were common prey of coconut crabs, this almost certainly would have been observed. Amerson (1969) and Berger (1981) report that both *Rattus rattus* and *R. exulans* eat bird eggs and young. Medina and Jackson (MS) found no evidence for this, but Temme (1982) reported that rats may have preyed on the eggs of *Sterna fuscata* on Aomon. The monitor lizard, *Varanus indicus*, is known to prey on birds and their eggs (Amerson, 1969), but because it is virtually certain that the population previously present on Japtan no longer exists, this potential predator is now gone. The return of the Marshallese population to Enewetak again makes man the major predator on birds at Enewetak.

Until the recent return of the Marshallese population to Enewetak, the major effect of man on the birds had been the alteration of the habitat by the fighting during World War II and the subsequent testing activities. The bird population of Enewetak certainly suffered during the battle in 1944 and thereafter when the atoll served as a staging area for campaigns farther to the west. The coconut palms and other vegetation were destroyed, and construction of the airfield and support facilities drastically reduced the

TABLE 1

Checklist of the Birds of Enewetak Atoll, Marshall Islands

Order PROCELLARIIFORMES	
Family PROCELLARIIDAE	
**Puffinus pacificus*	Wedge-tailed shearwater
Puffinus griseus	Sooty shearwater
Puffinus tenuirostris	Slender-billed shearwater
Pterodroma hypoleuca nigripennis	Black-winged petrel
Order PELICANIFORMES	
Family PHAETHONTIDAE	
**Phaethon rubricauda*	Red-tailed tropic bird
**Phaethon lepturus*	White-tailed tropic bird
Family SULIDAE	
**Sula sula*	Red-footed booby
**Sula leucogaster*	Brown booby
Family FREGATIDAE	
†*Fregata minor*	Great frigate bird
Order CICONIIFORMES	
Family ARDEIDAE	
**Egretta sacra*	Reef heron
Order ANSERIFORMES	
Family ANATIDAE	
Anas acuta	Pintail
Anas querquedula	Garganey teal
Order GALLIFORMES	
Family PHASIANIDAE	
†*Gallus gallus*	Jungle fowl or domestic chicken
Order CHARADRIIFORMES	
Family SCOLOPACIDAE	
Limosa lapponica baueri	Bar-tailed godwit
Numenius phaeopus	Whimbrel
Numenius tahitensis	Bristle-thighed curlew
Tringa glareola	Wood sandpiper
Family SCOLOPACIDAE (continued)	
Heteroscelus brevipes	Polynesian tattler
Heteroscelus incanus	Wandering tattler
Arenaria interpres	Ruddy turnstone
Gallinago hardwickii	Latham snipe
Calidris alba	Sanderling
Calidris acuminata	Sharp-tailed sandpiper
Calidris ruficollis	Rufous-necked sandpiper
Tryngites subruficollis	Buff-breasted sandpiper
Philomachus pugnax	Ruff
Family CHARADRIIDAE	
Charadrius dubius curonicus	Ring-necked plover
Charadrius mongolus	Mongolian plover
Pluvialis dominica fulva	Pacific golden plover
Pluvialis squatarola	Black-bellied plover
Family LARIDAE	
Sterna paradisaea	Arctic tern
**Sterna sumatrana*	Black-naped tern
†*Sterna lunata*	Gray-backed tern
**Sterna fuscata*	Sooty tern
**Thalasseus bergii*	Crested tern
†*Procelsterna cerulea*	Blue-gray noddy
**Anous stolidus*	Brown noddy
**Anous tenuirostris*	Black noddy
**Gygis alba*	White tern
Order CUCULIFORMES	
Family CUCULIDAE	
Eudynamis taitensis	Long-tailed cuckoo
Order STRIGIFORMES	
Family STRIGIDAE	
Asio flammeus	Short-eared owl

*Confirmed breeding bird.
†Believed to breed; confirmation needed.

ground cover. Many of the smaller islets remained basically untouched during that period, but with the advent of the testing program at Enewetak, major portions of the atoll were swept instantly by destruction.

The effects of the nuclear testing on bird populations has not been well documented, but certainly in those islands swept by blast and heat, the decimation of the bird populations must have been inevitable. Hines (1962) reports, for example, that after the first thermonuclear explosion at Enewetak (test Mike) in 1952, on Rigili (Leroy), some 14 miles from the blast site, "many of the terns there were sick, some grounded and reluctant to fly and some with singed feathers, particularly the noddy terns and the sooty terns, whose feathers are dark in color." At Bogallua (Alice) only 3 miles from ground zero, which previously had been "laden by stands of coconut palms and thickly populated by birds" (Hines, 1962), no animal life could be found. One week after the Mike test "transient birds" were observed on Engebi in a scene of utter desolation. Possible genetic effects on the birds apparently were not studied. On Janet Island on July 23, 1971, Berger found a white-tailed tropic bird chick with a deformed bill in which the lower mandible protruded far to the right of the normal upper mandible. This chick certainly died after parental feeding stopped. In a large colony of sooty terns on the same island, Berger found six immature terns with such badly deformed left wings that the birds could not fly.

Nevertheless, environmental alteration has not been totally negative with respect to all bird populations on Enewetak. The removal of vegetation from many of the islands as a result of the cleanup program has opened up new nesting areas for ground nesting birds, as documented by Temme (1979).

FEEDING HABITS

No intensive studies of the feeding habits of the seabirds of Enewetak Atoll have been published. Studies have been made, however, on many of the species in other parts of their range. For example, Ashmole and

Ashmole (1967) wrote that squid (family Ommastrephidae) and flying fish (Exocoetidae) were of primary importance to a colony of red-footed boobies that nest on the island of Oahu in the Hawaiian Islands. The same authors studied the feeding habits of seabirds on Christmas Island (Pacific Ocean) and concluded that flying fish and squid "are of outstanding importance in the diets of nearly all species of birds typical of the tropical Pacific." These findings were confirmed by Shreiber and Hensley (1976). Similarly, in his study of the sooty tern in the Hawaiian Islands, Brown (1973) found that the birds ate about half squid and half fish by weight. Four families of fishes were found in the diet, but the Carangidae (genus *Decapterus*) were the most important. It seems likely that the seabirds of Enewetak have similar feeding habits, even though some species tend to feed in the lagoon and others range far at sea in their search for food.

Drinking Saltwater

Fresh water is unavailable on most of the islands where seabirds nest, and the birds are adapted to drinking salt water. Not only do the birds not need fresh water, but Frings and Frings (1959) discovered that captive black-footed and Laysan albatrosses died unless they were fed adequate amounts of salt. All seabirds that have been studied possess special salt glands, located in the orbit, that secrete a fluid that has a higher salt concentration than that in seawater, thus leaving a net gain of water for the birds' physiological needs. The hypertonic solution that drains to the bill tip is discarded by head-shaking movements.

Guano Production

The excrement of seabirds, known as guano, is rich in phosphates and ammonium compounds (largely ammonium urate or uric acid). The input of nutrients of such guano to island soils can be great in nesting areas. At Enewetak there are recognizable deposits of bird guano in the *Pisonia* stands on the southwestern islands, from Igurin to Rigili. Richardson (MS) reported that at Rongelap Atoll there was "a relationship between the greatest concentration of breeding birds, the most extensive stands of large trees, and the best-developed soils." On Kabelle Island he estimated that the 1400 to 1800 birds of three tern species contributed over 40,000 kg yr^{-1} of waste to this island of 2400 square meters.

Murphy (1936) said that a single Peruvian booby *(Sula variegatus)* produces as much as 150 g d^{-1} of guano, and that, if 30 g of this were deposited on an island, a thousand birds would produce more than 10 metric tons a year. He added that Peruvian booby guano is more than 33 times as effective as barnyard manure. However, whether the guano accumulates in large quantities or is leached depends on climatic conditions, that is, the amount and pattern of rainfall. Nevertheless, the guano input has a profound effect both on the plant life of the islands and on the lagoon and ocean surrounding them. For example, Hutchinson (1950) describes these effects as follows: "If a bird colony is situated on such a coast or island, part of the upwelling nutrients will finally be deposited on the island. Wherever any of this material is washed back by rain or wave action into the sea, there will be locally and momentarily a much greater concentration of nutrients where the guano solution returns to the ocean than at any other place. The result of a very large bird colony on a section of coastline or on an island, whenever climatic conditions and the form of the substrate of the colony permit guano to be returned to the ocean, will be to steepen the nutrient gradient. Nutrient elements that, without the birds, would tend to remain in the bodies of the fish in the peripheral part of the trophophoric field of the colony and on the death of the fish would presumably be distributed widely throughout the general circulation of the ocean are concentrated by the birds on and around the island. The result will be increased littoral productivity and probably increased littoral fish production. If the latter occurs, the birds will not have to move so far out to sea for their food, and a steady-state condition will be set up. . . . It is, in fact, conceivable that large bird colonies, far from reducing the commercial catch of fish by competition, may actually increase the catch by a process of biogeochemical concentration." Also related to this situation are the excreta voided in flight by the many thousands of seabirds as they fly over the lagoons and the ocean on their way to and from the feeding grounds.

BREEDING HABITS

Many of the seabirds or oceanic birds are called pelagic species because they spend most of the nonbreeding season on the open ocean, returning to islands only for the nesting season. Some species do not reach sexual maturity for several years (e.g., until about 5 years of age for the frigate bird and black-footed albatross), and they may remain at sea during this period. Certain species (e.g., brown booby, sooty tern) lay their eggs on the ground; some excavate burrows in the sand or other substrate (e.g., wedge-tailed shearwater); and others (e.g., red-footed booby, black noddy) typically build a nest in some kind of vegetation, although this may place the nest only a foot or so off the ground. Most seabirds lay a single egg in a clutch, but the clutch of the brown booby usually contains two eggs.

On both lava and coral islands, nesting adults are subjected to excessive heat and solar radiation that are counteracted by physiological and behavioral adaptations. Birds do not have sweat glands, and both adults and young birds dissipate excess heat by evaporative cooling. This is accomplished either by panting or by gular flattering, that is, by rapidly vibrating the throat and floor of the mouth, thus speeding up blood flow and loss of heat through the membranes in the floor of the mouth and throat (gular) areas. Because of the heat stress, the adult bird often must stand over the egg or recently hatched chick to provide

shade for it. Chicks also seek the shade of vegetation when available.

Unfortunately, little precise information is available on the nesting activities of the birds of Enewetak Atoll. No definitive studies have been made on any of the 12 species of breeding birds; still awaited is proof of nesting by the four species of "possible breeders."

More has been written about the distribution and nesting of the sooty tern on Enewetak than on all other species together. There now appears to be either one or two nesting colonies of sooty terns at Enewetak, and there is considerable historical evidence that the birds shift their nesting sites from island to island. For example, Richardson (MS) observed a colony of sooty terns on Aej (Olive) during February 1959, but none was found at that islet during the summer of 1965. Carpenter et al. (1968) estimated a colony of 16,000 terns on Lujor (Pearl) in 1966, but a year later the colony was found on Luoj (Daisy) more than 10 miles away. Berger found the only large colony of sooty terns on Janet Island during the third week of July 1971.

Temme (1979) reports that in November 1977, there were about 10,000 sooty terns nesting on Aomon (Sally) in an area cleared only a short time before; when crowded, the nests are closely packed with 25 to 30 eggs per square meter. The following March an estimated 5000 adult and immature birds were there, with a few nests containing eggs. During Temme's visit only a few hundred additional sooty terns were observed on the 14 other islands visited. However, during November 1978, an estimated 29,000 adults, 7800 chicks, and 6700 eggs were present on Boken (Irene).

In the Hawaiian Islands, William Y. Brown determined an incubation time of between 28 and 31 days. The young terns first fly when they are about 57 days old, usually leaving the island during the day but returning to it to be fed by the adults at night (Berger, 1981).

Because no data are available for consecutive 12-month periods and for several consecutive years, only problems for study—rather than conclusions—can be suggested. The shift of nesting populations of sooty terns from island to island in different years apparently is partly a function of vegetation removal and/or regrowth. This tern nests on the ground in open areas, often where scattered patches of grasses and other low-growing vegetation are interspersed with open sand or coral.

In the Hawaiian Islands, the brown noddy nests on the ground; at Enewetak, however, this noddy also often builds a nest in scrub vegetation (e.g., *Scaevola*, *Pisonia*, *Tournefortia*) or even in coconut trees. According to Robert K. Bastian (MS), the nest of the brown noddy at Enewetak contains sticks, leaves, grasses, feathers, driftwood, gravel, algae, sponge, and, characteristically, coral and shell fragments.

In most parts of its range, the black noddy builds a bracket-like nest in shrubs and trees, but Atlantic Ocean populations usually nest on cliff ledges and offshore stacks, where the birds are safe from mammalian predators. At Enewetak nests usually are built in trees (especially *Tournefortia* and *Pisonia*). The nests lack the coral and shell fragments of the brown noddy and usually are composed largely of seaweed and accumulations of feathers and guano.

A great deal needs to be learned about the breeding seasons for each species and for the apparent variation in nesting seasons, especially for the sooty tern. Carpenter et al. (1968) noted that: "The 1959 and 1962 colonies were breeding in the March to May period; the 1966 colony was breeding in the July to September period; in 1967, in June and July. A satisfactory reason for the apparent variation on Eniwetok does not seem to exist, though food supply, precipitation, or even vegetational appearance may be factors." A thorough study of the sooty tern at Enewetak would be revealing; in other parts of its range, the sooty tern nests at 6-, 9-, or 12-month intervals (Ashmole, 1965; Kikkawa, 1976). An intensive study of banded birds will be needed to determine the pattern at Enewetak.

The white tern is one of the most interesting species at Enewetak and one that occurs on most of the islets of the atoll. This tern does not build a nest and usually lays its single elliptical egg on a bare, horizontal branch of a tree or shrub, sometimes in the deserted nest of a noddy tern (Figs. 1 and 2). Carpenter et al. (1968) estimated the population of white terns to be about 1400 birds for Enewetak Atoll in 1966; they found the largest concentration on Libiron Islet. I found the densest populations on James (Libiron) and Irwin islets during the third week of July 1971. Many adults were incubating eggs, but there also were young birds ranging from newly hatched to those just capable of flight.

THE REEF HERON

The reef heron *(Egretta sacra)* has a wide range that includes Korea, Japan, Malaysia, Australia, Melanisia, Polynesia, and Micronesia. It is the only heron found at Enewetak. It occurs in three color phases: white, gray, and mottled. Most immature birds have the mottled plumage. Of 57 herons observed by Carpenter et al. (1968), 48% were white, 28% were gray, and 24% were mottled. Pearson and Knudsen (1967) reported a 20:30:50 ratio. Slater (1971) notes that the "white phase predominates in the centre of its range and the grey phase on the periphery."

The reef heron nests on many of the islets of Enewetak, on or near the ground. The birds apparently nest singly, with a clutch of three eggs. Carpenter et al. (1968) found "all stages from eggs to fledgling young" during June. These herons feed largely on fish and crabs. Carpenter notes that "the preferred feeding location was the reef and abandoned landing craft."

REGULAR MIGRANTS AND ACCIDENTALS

Many shorebirds that nest in Alaska and Siberia winter on islands in the Pacific Ocean. At least 17 species have been recorded at Enewetak. Some of these have been dis-

Fig. 1 White tern egg on a dead branch, James Island, July 27, 1971. [Photograph by A. J. Berger.]

Fig. 2 White terns in flight, Tilda Island, July 24, 1971. [Photograph by A. J. Berger.]

cussed in detail by Johnson (1973, 1977, and 1979), by Johnson and Morton (1976), and by Hailman (1979). Many other species have been recorded in Micronesia (Baker, 1951; Owen, 1977), and some of these certainly will be found at Enewetak when more intensive field work is done there.

Several of the wintering shorebirds remain as nonbreeding individuals during the northern summer breeding season. Johnson and Morton (1976) and Johnson (1979) discussed this phenomenon for five species. They thought that such summering birds were first-year birds that lacked the physiological stimulus for migration. Some

of the birds that Johnson examined exhibited partial or even complete breeding plumages although the birds were biologically immature. "Fat content in summering birds varies from around 3 to 6 percent of body weight, restricting them to relatively short flights." Johnson also wrote that ". . .the sex ratio of plovers was strongly biased toward males (about 5:1), and apparently balanced in the other species" (whimbrels, bristle-thighed curlews, wandering tattlers, and ruddy turnstones).

Johnson and Kienholz (1975) collected a female short-eared owl *(Asio flammeus)* on Fred islet on July 7, 1973. Earlier, Amerson (1969) wrote that there were no records for owls in either the Marshall or the Gilbert Islands. The subspecies for the collected female was not determined; hence, the general origin of this accidental visitor is unknown.

Hailman (1979) discussed several sightings of birds for which species identification was not possible; these birds on the hypothetical list include a duck *(Anas)* and a tern (presumably of the genus *Sterna*).

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